PREDICTING RATES AND PATTERNS OF ALIEN PLANT SPREAD

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Abstract.

The invasion of alien plants into natural ecosystems is a widespread phenomenon that impacts negatively on ecosystem structure and functioning. The invasion and subsequent spread of an alien plant population is equivalent to the processes of colonisation and migration. This implies that the existing toolbox of techniques developed for plant succession research should be useful for predicting plant invasions. Practitioners of invasion biology have, however, found biological invasions frustratingly difficult to predict. The aim of this thesis was to use succession models to develop a modelling protocol for predicting rates and patterns of alien plant spread. The rationale was that such a model would both improve our understanding of the determinants of invasions and allow us to make predictions on the rates and patterns of alien plant spread. Such predictions are likely to be extremely valuable for the tactical and strategic management of plant invasions. Many modelling approaches could be adopted: the need to transcend the gap from general models of plant spread to management models led me to select a spatially explicit simulation modelling approach.

The modelling approach is developed by comparing the behaviour of an individual based spatially explicit simulation (SEIBS) model of plant spread to the behaviour of the classic Skellam reaction diffusion model. This process also served to define the model's sensitivity and data requirements. The model's heuristic value is demonstrated by exploring why it is so difficult to predict which plant will invade which environment. The model also provides a useful tool for exploring the role of long-distance dispersal in determining invasion rates. I show that long-distance dispersal is extremely difficult to define statistically, but is a key determinant of invasion rates. The model is validated using independent data on the spatial demography of two invasive species, *Acacia cyclops* and *Pinus pinaster,* and independent historical reconstructions of invasions. This validated model was then used to develop a dynamic landscape-extent model. This scaled-up model explores the optimal strategies for clearing alien plants and the ability of different clearing strategies and funding schedules to mitigate the threat that alien plants pose to native species.

I conclude that models that are tightly linked to understanding of ecological processes and to field data can be used to rapidly develop predictive models. The development of these models challenges our fundamental ecological understanding and, therefore, emphasises the interplay between data, theory and prediction.

Keywords: plant spread, plant migration, invasion, colonisation, alien plants, succession, disturbance, life history attributes, dispersal, recruitment, mortality, scaling, individual based modelling, spatially explicit modelling, mechanistic modelling, cellular automata, logistic regression, prediction, validation, management models, fragmentation, long-distance dispersal, error-analysis, conservation biology, theoretical ecology, invasion biology.

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CHAPTER 1

INTRODUCTION: PREDICTING RATES AND PATTERNS OF ALIEN PLANT SPREAD

THESIS STUCTURE

This thesis is presented as a series of scientific papers, each of which was written to exist as an independent scientific product. This means that each chapter develops its own rationale, sets its own aims and draws its own conclusions. In effect this also means that each chapter touches on issues that are not central to the thesis; these by-products are nonetheless contributions to science and are included in the thesis. Despite this independence this thesis is tightly structured and each chapter is a step in the development of a protocol for predicting rates and patterns of exotic plant invasions. This opening chapter outlines the broad objectives of the thesis and provides an overview of the thesis structure.

BACKGROUND AND OBJECTIVES

This thesis aims to develop a protocol for predicting the rates and patterns of alien plant spread across landscapes. I do not review the dire consequences that alien plant invasions have had on ecosystems throughout the world; these have been adequately and repeatedly reviewed (e.g. Groves and Burdon 1986, Macdonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989, di Castri et al. 1990, Lodge 1993, Williamson et al. 1996, Vitousek et al. 1996, Simberloff et al. 1997). Suffice to mention that alien plant invasions can alter the functioning of natural ecosystems and increase the risk of extinction of native species. It follows that invasions have negative impacts on the functioning of ecological-economic systems (Higgins et al. 1997) and that an ability to predict the spatial and temporal locations of alien plants would be useful for conservation planners, land managers and environmental policy makers.

When this thesis was initiated, no protocol for predicting the spread of alien plant species across landscapes existed. The approach taken was to adopt and adapt the techniques for modelling plant succession for modelling alien plant spread. This was motivated by three observations. First, an approach that concentrates on the processes of invasions would be of greater benefit to our understanding of invasions than a statistical approach. Second, the

mechanisms of alien plant invasion and spread are the same as the mechanisms of native plant succession and migration. Third, invasions are natural experiments: if the tools of plant succession theory are useful they should be able to predict which species will invade under which conditions.

The invasion of the fynbos biome, South Africa, by alien trees and shrubs served as the case study for the dissertation. Fynbos invasions are a useful case study because the natural history of these invasions were well understood at the outset of this project (Richardson et al. 1992). The invasion of fynbos by alien trees and shrubs are also relatively simple: the invasion process is driven by fire-stimulated recruitment events and factors such as resource gradients, allee effects, herbivory, inter-specific competition, mycrorrhizal associations, while of importance in other invasions, are of limited importance in fynbos invasions. The devastating impact of alien plants on fynbos landscapes also meant that predictions of future distributions of these plants would be immediately useful for planning alien plant control operations and for motivating funds for alien plant control.

OVERVIEW

The chapters of the thesis develop a protocol for predicting rates and patterns of exotic plant invasions. The first task was to select an appropriate technique for modelling plant spread (Chapter 2). This is an important decision as it determines the empirical data requirements for the model as well as type and scale of predictions. Since I was interested in a mechanistic and not statistical model of invasion, the choice lay between spatially explicit simulation models and reaction diffusion models. The advantage of using reaction diffusion models is that their behaviour is well understood, and they have been widely applied in invasion contexts. However, they are inflexible and perhaps inappropriate for simulating the spatial dynamics of event driven systems like fynbos. For this reason we selected the simulation approach. Essentially this decision allowed the use of the same core model for both general and applied applications. Although spatially explicit simulation models existed when this study started, none had been applied to modelling plant invasions or plant spread. The third chapter developed a simple spatially explicit, individual based simulation (SEIBS) model of plant spread and compared its behaviour to the reaction-diffusion model developed by Skellam (1951). Chapter 3 shows how life history attributes and fire frequency interacted to influence the rate of spread of a migrating plant population; it does not explicitly explore the conditions under which an invasion would succeed or fail. Chapter 4 explores this question in

more detail. It particular this chapter explores how interactions between life-history attributes, environment type and disturbance level challenges the predictive ability of correlative models. This chapter in effect defines a protocol for defining an invasive plant's perspective of assembly rules (Keddy 1992). A comparison of the SEIBS model's predictions of spread rates (Chapter 3) with empirical spread rates suggested that dispersal was not being modelled adequately. Chapter 5 explores the nature of this problem in detail by examining our limited ability to develop empirical estimates of rare long-distance dispersal events. Chapter 5 completes the development of the SEIBS model and Chapter 6 aims to validate the SEIBS model. Model validation involved the collection of empirical data on the spatial recruitment dynamics of alien plant invasions. Sequential aerial photographs were used to reconstruct invasion histories at several independent sites. An error analysis was used to evaluate the performance of the model and the predictions of the model agreed well with the historical reconstructions.

The next step was to scale up from the fine-grained SEIBS model to a coarser-grained landscape-extent model. The rationale for developing the spatially-explicit, landscape-extent simulation (SELES) model was to develop a dynamic, decision making tool for planning and motivating for alien plant control. The SELES model aggregates the fine grain behaviour of the SEIBS model into a coarser grained framework and integrates landscape levels sub-models. The first sub-model is a statistical description of site suitability; the process of defining these sub-models is described in Chapter 7. The second landscape level sub-model is a simple fire spread model. Chapter 8 describes the fire spread model and scaling up of the SEIBS model into the SELES framework. The usefulness of the SELES model is demonstrated by exploring several management scenarios.

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CHAPTER 2

A REVIEW OF MODELS OF ALIEN PLANT SPREAD

Abstract. Alien plants invade many ecosystems worldwide, often having substantial negative effects on ecosystem structure and functioning. The apparent complexity of invasions has impaired the development of a predictive framework of alien plant spread. Such a framework requires both a conceptual understanding of the ecology of invasions and appropriate modelling tools. I demonstrate, using a simple conceptual model and illustrative examples from the literature, that a predictive understanding of invasions can be established. Potential modelling tools are reviewed by categorising models of plant spread as simple-demographic, spatial-phenomenological or spatial-mechanistic. The assumptions, predictive potential, knowledge and data requirements of these modelling tools are discussed in the context of selecting the most appropriate alien plant spread model for a given case.

Key words: Biological invasions, prediction, modelling.

INTRODUCTION

Alien plants have invaded many different ecosystems in almost every part of the world (Drake et al. 1989). The negative impacts that alien plants have on ecosystem structure and functioning means that their presence is often incompatible with the ideals of sustainable management or conservation. Important impacts of alien plants include altered soil nutrient status (e.g. Vitousek and Walker 1989, Musil 1993), reduced recruitment of native plants (e.g. Richardson et al. 1989, Walker and Vitousek 1991), altered fire regimes (e.g. van Wilgen and Richardson 1985, Christensen and Burrows 1986) and reduced stream-flow from catchments (van Wilgen et al. 1992).

Research on invasive alien plants has been motivated by the need to mitigate their negative influence on natural systems, and by the unique theoretical opportunities provided by the expansion of an alien organism into a new range. From a theoretical perspective, invasions provide large-scale natural experiments, which offer insights into issues fundamental to ecological theory. For example, in invasions dispersal and immigration, and not just birth and death, are recognised as the primary determinants of demographic performance (Harper 1977, Mack 1985, Kruckeberg 1986). In addition, invasions provide unique examples of the

importance of predation and competition in determining population and community dynamics (Mack 1985, Lodge 1993) since they represent natural experiments where many interspecific competitors and specialist herbivores have been removed. Conversely, the effects of individual species on ecosystem-level phenomena can be unambiguously illustrated in invasions (Vitousek and Walker 1989).

Recent reviews of biological invasions (e.g. Groves and Burdon 1986, Macdonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989, di Castri et al. 1990, Richardson et al. 1992, Lodge 1993) indicate that research has concentrated on the collation of the attributes of invasive organisms and the environments they invade through the examination of case studies. The aim of this approach has been to identify the types of environments and organisms that are likely to produce invasions, thereby developing a global database for the proactive management of invasions. Unfortunately this comparative approach has produced few global generalisations and consequently, its potential for managing and preventing invasions is limited (Lodge 1993). This lack of global generality has created the impression that invasions cannot easily be predicted using mathematical models (Williamson and Brown 1986). Recent work (Richardson et al. 1990, Richardson and Cowling 1992) has, however, illustrated that the profiles of invasive species can emerge from comparative analyses of the life history attributes of invasive species in particular environments. This suggests that prediction and, therefore, the mitigation of existing invasions and the prevention of future invasions are possible, at least in some systems. Consequently, some framework for the quantitative prediction of plant invasions is required.

A framework for the prediction of alien plant spread requires *inter alia* the development and refinement of mathematical modelling tools. By reviewing approaches of modelling plant spread, this chapter aims to provide an overview of the tools available for generating the information required for predicting plant invasions. In particular, I aim to (1): conceptually define what constitutes a plant invasion by reviewing the factors which influence alien plant spread, thereby identifying the information requirements for modelling the spread of alien plants; and (2): identify the tools available for modelling alien plant spread by reviewing the historical application of plant spread models and models which have potential for the prediction of plant spread.

A CONCEPTUAL MODEL OF ALIEN PLANT SPREAD

A conceptual model of plant spread can be used to provide a framework for the identification of the factors that influence the performance of invading populations. Since most mathematical models use relationships between parameters and variables as an abstraction of some ecological processes, a conceptual understanding of invasion processes is imperative. A simple conceptual model that consists of four main components (Figure 1) can describe the features of plant invasions. The central component of the model, the *demographic processes*, determines the output component, *alien abundance*. The demographic processes are determined by the interaction between *autecological attributes* and *environmental resource fluctuations*. These components are discussed more fully below.

2.2.1. Autecological attributes

The importance of autecological attributes in determining plant distribution patterns is not unique to invasion scenarios, but is an established principle of plant succession theory (e.g. Noble and Slatyer 1980, Chapin et al. 1994). Although *autecological attributes* could potentially include any attribute of a plant's ecology, our interest is in the attributes that determine invasive success. Many alien invasion case studies attribute invasive success to some aspect of a plant's autecology such as life history or ecophysiological attributes. Invasive success has, for example, been attributed to the nitrogen-fixing ability of *Myrica faya*, which invades the

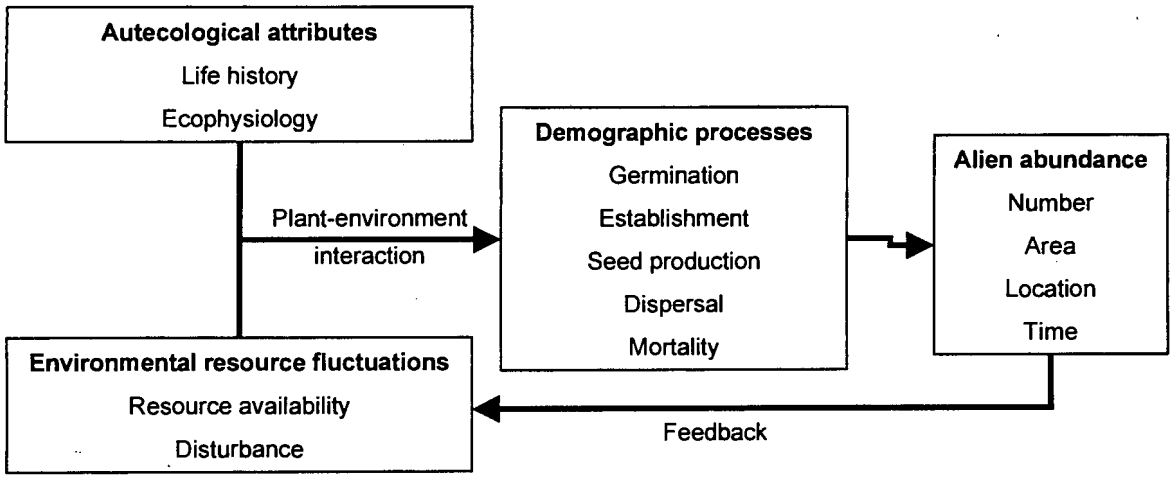

Figure 2.1. A conceptual model of alien plant spread (see text for details).

Hawaiian islands (Vitousek 1990), and the short juvenile periods of alien *Acacia* species in fynbos, South Africa (Richardson et al. 1992). More often, a suite of life history attributes is implicated in invasive success. Richardson and Cowling (1992), for instance, argued that short juvenile periods, large and serotinous seed banks and highly dispersable seeds are a suite of attributes that appear to guarantee invasive success in fire prone mountain fynbos. Although these examples illustrate that a plant's autecological attributes are undoubtedly important determinants of invasive success, no attribute or suite of attributes has emerged as a global guarantee of invasive success (Lodge 1993).

Environmental resource fluctuations

A consideration of the environmental context of invasion scenarios serves to illustrate why a global recipe for invasive success does not exist. Since environments differ in their spatial and temporal patterns of resource supply (O'Neill et al. 1986), the opportunities they provide for recruitment and spread differs substantially. Hence both the biotic and abiotic properties of the target habitat are likely to be as important as the autecological attributes of the invading species in influencing invasive success. The invasion-window concept (Johnstone 1986) emphasises the importance of the temporal availability of resources in influencing invasive success. Equally important, however, is the spatial pattern of resource availability.

The environmental resource supply can be divided into two categories: *resource availability* and *disturbance* (Figure 1). Resource availability includes factors such as nutrient, moisture and space availability, which can be regarded as manifestations of spatial and temporal environmental heterogeneity. The importance of environmental heterogeneity in influencing invasion patterns is well established. For example, Lonsdale (1993) observed a strong correlation between the spread rate of *Mimosa pigra* in a tropical wetland of northern Australia and the previous year's rainfall. Similarly, Williams et al. (1987) noted that establishment of *Baccharis pilularis* ssp. *consanguinea* in a northern California grassland was correlated with annual and spring rainfall. In another example, nutrient availability strongly influenced the invasibility of a Californian serpentine grassland by alien annual grasses (Hobbs et al. 1988, Huenneke et al. 1990). Both biotic and abiotic attributes of the environment were experimentally shown to govern the invasibility of a Californian coastal plant community (D'Antonio 1993). The same was illustrated more indirectly in a multiple regression analysis which related a number of habitat and land-use attributes to the distribution and spread of the invasive shrub *Rhododendron ponticum* in North Wales (Thomson et al. 1993).

Disturbances can be defined as resource fluctuations that are discrete relative to the temporal scale of investigation (White and Pickett 1985). Fire in South African fynbos is an example of a disturbance: in a relatively discrete event, a fire creates the space in which alien trees can establish (Richardson and Cowling 1992). The role of disturbance in influencing invasive success is unanimously recognised; indeed Fox and Fox (1986) concluded, "there is no invasion of natural communities without disturbance". Although anthropogenically modified disturbance regimes have, in particular, been implicated as invasion facilitators (Fox and Fox 1986, Hobbs and Huenneke 1992), invasions can occur under a natural disturbance regime (e.g. Richardson et al. 1992). Experimental studies have also illustrated the role of disturbance in invasions. For example, Hobbs (1989) showed that the presence of disturbed areas could enhance the establishment rate of alien plants. Similarly, Bergelson et al. (1993) found that the area and spatial distribution of disturbed areas influenced invasive plant spread. Invasion case studies, through the use of correlative evidence have, like the experimental studies, also implicated disturbance. For example, DeFarrari and Naiman (1994) concluded from an alien plant survey that disturbance type and time since disturbance were the major factors influencing invasibility in Washington, USA. In another survey 90% of the alien species on Lord Howe Island, Australia, were associated with disturbed areas (Pickard 1984). Similarly, Crawley's (1987) analysis of floristic data of the British Isles revealed that aliens constituted more than 50% of the flora in highly disturbed areas, but less than 5% of the native woodland flora.

Plant – environment interaction

The literature reviewed above shows that both plant and environmental factors influence invasions, yet neither, in isolation, provides a blueprint for invasive success. The fact that seed production and seed bank accumulation rates can be orders of magnitude higher in novel environments than in native environments (e.g. Gill and Neser 1984, Weiss and Milton 1984, Honig et al. 1992), supports the observation that the interactions between a plant and its environment are crucial in invasions. It follows that a predictive knowledge of invasions lies in the understanding of how autecological performance and resource supply patterns interact to influence the variables and parameters of plant spread models.

In order to define the plant-environment interaction, it is useful to consider the environment as a series of filters which prevent unsuited plants from establishing, maturing, reproducing and dispersing (Keddy 1992). The selection of the appropriate autecological attributes and

environmental filters requires an understanding of how the system functions. The successful spread of *Rhododendron ponticum* through the oakwoods of Ireland provides an example. Safe sites for establishment are created by herbivore disturbance and by the successionary sequence of the bryophyte understorey (Cross 1981). *Rhododendron* competes with native species for these sites, but because it is both shade-tolerant and unpalatable (a trait combination not found in the native flora), its successful recruitment is ensured in the heavily grazed understorey (Cross 1981).

From demography to alien abundance

Once a conceptual understanding of an invasion has been arrived at, it needs to be translated into quantitative demographic variables, which will allow the estimation of alien abundance. In practice, we make assumptions about plant - environment interactions that allow us to develop models and make predictions of alien abundance. Different models have different procedures for dealing with the ecological realism of plant - environment interactions and hence of abstracting this realism into input parameters and, ultimately, future alien abundance.

Alien abundance may be any measure of abundance (e.g. presence-absence, frequency, basal cover, aerial cover, or biomass). Which measure is most appropriate will be determined by the study's objectives. Ideally, the measure of abundance should include spatial and temporal co-ordinates as well as a description of the spatial pattern of the invasion (e.g. Wilson and Lee 1989). Spatial and temporal co-ordinates are likely to be useful for linking invasion studies to theoretical models of spatial population dynamics (Levin 1992) and for planning management actions.

Feedback

The conceptual model also includes the feedback effect of alien abundance on resource fluctuations. This feedback may either accelerate or retard invasive spread and consequently should be included in alien spread models. For instance, dense stands of the alien shrub *Hakea sericea* in mountain fynbos can substantially increase the intensity of fires (Richardson and van Wilgen 1986). Similarly, the invasion of alien C_4 grasses (e.g. *Melinis minutiflora*, *Andropogon virginicus* and *Schizachyrium condensatum*) in the Hawaiian islands has led to an increase in the frequency and intensity of fires, this has facilitated invasion rates and has substantially altered the natural ecosystem's characteristics (Hughes et al. 1991).

The model presented here has used information gained from invasion case histories and ecological theory to generate a conceptualisation of the spread of an invasive plant into a target landscape. The model emphasises that attributes of the plant and the environment being invaded are needed to predict plant invasive plant spread. It does not, however, prescribe which attributes are most important or how the ecological knowledge is used, conceptually or mathematically; these issues will be dealt with in the next sections.

PREDICTIVE MODELS OF PLANT SPREAD

Here I review some of the more prominent models that have been applied to plant invasions and discuss other models that have obvious potential for this purpose, but have to the best of our knowledge not been applied in an invasion context. As a framework for discussion I assign plant invasion models to three categories: simple-demographic models, spatial-phenomenological models and spatial-mechanistic models (Table 2.1). This categorisation is based on the model's input requirements, its data sources and its output variables. Input parameters and variables are defined according to the response variables they influence and whether they have any intuitive ecological meaning. The data sources used to parameterise the model are distinguished as either being from historical records (e.g. floristic databases) or from independent sources (e.g. field and laboratory trials). The hierarchical level of the data source relative to that of the output (e.g. the use of autecological information to make forecasts at a landscape scale) and the types of output the models produce are also used to distinguish between model types.

Table 2.1. The characteristics of three types of plant spread models

Model type	Type of input	Type of data source	Type of output
Simple-demographic	Ecologically meaningful Influences birth and death	Independent Lower hierarchical level	Population density, Time
Spatial-phenomenological	No ecological meaning Influences area occupied	Historical Same hierarchical level	Area, time
Spatial-mechanistic	Ecologically meaningful Influences birth,death, dispersal	Independent Lower hierarchical level	Population density Area, time

Simple-demographic models

Demographic models aim to predict the future number of individuals in a population. They do this by making assumptions about the nature of population growth and by estimating demographic parameters regarded as being important in determining population dynamics. The models presented in this section are generally not regarded as invasion models *per se*, but are discussed here since they represent the theoretical foundation of invasion models and are often incorporated (with their underlying assumptions) into 'true' invasion models. In particular, simple-demographic models provide the tools for forecasting the likelihood of population establishment, the probability of local population extinction and population density. In situations where the rate of invasion is determined primarily by the population's reproductive rate, simple-demographic models may be adequate forecasting tools (Hengeveld 1989).

Exponential model

The most basic demographic model is the exponential model, which assumes an exponential rate of population growth. It is mostly represented by the differential equation

$$\frac{dN}{dt} = rN \qquad (1)$$

where N is the population size at time t. The parameter r is the intrinsic rate of population growth, which integrates fecundity, survivorship and development rate. Typically, r is estimated from empirical data sources, for example life table data generated in predefined environmental conditions. Despite its ubiquity in population models, few adequate estimates of r exist for plants (Crawley 1983, but see Silvertown et al. 1993). Techniques for estimating r are not standard and this often inhibits the successful application of simple demographic models (Williamson 1989). Conceptually, r represents the combined effect of the life history attributes of individual plants on the population's reproductive potential under particular conditions (Williamson 1972). It follows that estimates of r generated from information of a plant's performance in its native environment would be of limited use in an invasion model.

Logistic model

The exponential model assumes that environmental resources are infinite, that is it assumes no density-dependent effects on population growth. In the logistic model population growth is assumed to be a function of the total population size and the maximum equilibrium population size, such that

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \qquad (2)$$

where K is the equilibrium population size, or the population size at which the average change in population size is zero. Hence, K limits population growth, especially at high population densities. The equilibrium population size is either estimated from empirical sources or from estimates of resource availability and resource consumption rates. Although K cannot be directly measured or predicted, it conceptually represents the number of individuals that can survive on some limiting resource.

Logistic-difference model

The exponential and logistic models assume that both time and population size are continuous variables. Since the number of individuals in real populations is an integer, a model that considers these two variables as integers (i.e. discrete variables) may be more appropriate. Discrete variables are recommended when the number of individuals in the population is small, when generations do not overlap, or when reproduction and mortality are not continuous. Difference equations allow both the numbers of individuals in the population (N) and time (t) to be treated as discrete variables. A discrete analogue of the logistic model can be represented as

$$N_{t+1} = N_t[1 + r(1 - \frac{N_t}{K})] \qquad (3)$$

where N_{t+1} is the integer number of individuals in the population at time + 1. The mathematics of continuous situations are generally better developed than that of the analogous discrete situation. However since discrete time models are easier to incorporate into computer algorithms, the discrete formulation is often preferred.

Stochastic model

The exponential, logistic and logistic-difference models assume that environmental conditions are constant in time and that there is no variance in the behaviour of the population. Variability is a ubiquitous feature of natural systems and there are situations where variability influences both the quantitative and qualitative performance of models (Burgman et al. 1993). Models that account for variability by incorporating random variation into model parameters are referred to as stochastic models. The simplest way of incorporating stochasticity is to allow the rate of increase (r) to vary as a function of some random variable; the logistic-difference model then becomes

$$N_{t+1} = N_t + N_t(r + y_t) - r\frac{N_t^2}{K} \qquad (4)$$

where y_t is a random variable with a mean of 0 and a variance of 1. Comparisons between deterministic and stochastic population models suggest that a stochastic model will always predict a lower population size than its deterministic analogue, and that the magnitude of this difference will be a function of the variance of the random variable and the initial population size (Burgman et al. 1988). In addition, since the chances of population extinction increases with the variance of the population growth rate and with the inverse of the population size, it follows that stochastic models are likely to be useful when population sizes are small, as is the case early in an invasion (Mollison 1986).

The application of demographic models to invasions

Many modifications to demographic models can be found; these are usually applied when the underlying assumptions of the model are no longer satisfactory. Crawley (1986), in reviewing the demographic features of invasive organisms, concluded that since there is no clear demographic profile of a successful invader, simple demographic models are unlikely to be useful. This motivated him to propose a complicated demographic invasion model, considered as "the minimum level of complexity consistent with the aim" of predicting invasions (Crawley 1986). The model includes many parameters that interact to reduce r and thereby retard invasions. Processes accounted for in Crawley's model include interference competition (a function of competitors), exploitation competition (a function of the resource supply rate), the influence of natural enemies (a function of alternate prey items), the lack of mutualists, and immigration (Crawley 1986). Because data for most of the parameters in Crawley's model are

not available for most species and environments (and would be difficult and time-consuming to collect), this model has limited practical use. Despite being a complex parameter-rich model (see Williamson 1989, Wissel 1992a for criticisms), Crawley's (1986) model proposes using estimates of *r* obtained from the invasive organism's native environment and information about the receiving environment to estimate a reduction in *r* caused by interference and exploitation competition, natural enemies and a lack of mutualists. Performing demographic trials in the receiving environment would be a simpler way of estimating the population's demographic potential or invasive risk for a given environment (cf. Peters 1992).

Spatial-phenomenological models

The number of individuals present in a population is undoubtedly important in forecasting invasion events, especially in the early stages of an invasion when population sizes are small and the risk of extinction is large (Williamson 1989). However, the area occupied by the invasive population is a key dimension of an invasion. Since invaded ecosystems have different attributes to uninvaded ecosystems, the area of land occupied and the rate of this occupation needs to be quantified. This observation has led to the development of a number of models aimed at the prediction of the area invaded. The spatial models considered in this section are referred to as phenomenological models because they invoke no ecological mechanism as a means to prediction. These models therefore assume that plant - environment interactions are best described by empirically derived constants.

Regression models

The simplest spatial models adopt a regression approach, where investigators use historical records to quantify the relationship between area invaded and time. Perrins et al. (1993) examined the rate and extent of spread of three introduced *Impatiens* species in the British Isles. Historical records were used to count the number of sites occupied by each of the three species at 20 year intervals. These empirical data were then fitted to logistic curves, recognising that the number of available sites limits invasive spread. The logistic curves and assumptions regarding the shape and size of the sites were used to estimate the initial and maximum rates of spread of the three species.

Pysek and Prach (1993) used floristic records to reconstruct the cumulative number of localities invaded over time by four plant species (*Impatiens glandulifera, Heracleum mantegazzianum,*

Reynourtia japonica and *R. sachalinensis*) which are alien to central Europe. An exponential regression model was fitted to the data and the slope of the regression was used as an estimate of the invasion rate. Lonsdale (1993) applied a similar regression approach, using empirical data generated from aerial photograph interpretation to estimate the spread of *Mimosa pigra* in a tropical wetland of northern Australia. In the last two cases regression models were used that assumed that space did not limit the rate of spread (cf. Perrins et al. 1993). This assumption is only acceptable in the early phases of an invasion, when the area available for invasion is relatively high.

An alternative application of the regression approach was implemented in an investigation of the spread of *Olearia lyallii* on the subantarctic Auckland Islands, New Zealand (Lee, et al. 1991). Multiple regression techniques were used to identify the environmental preferences of *Olearia*. These regressions were then used to predict the potential basal area of *Olearia* in sites outside its present range. However, no estimates of how long *Olearia* would take to realise its potential range were made.

Geometrical models

Moody and Mack (1988) developed a phenomenological simulation model of plant spread which considered a number of independent foci expanding radially on a large, homogenous, two-dimensional plane. The principal model parameters are the rate of expansion of the foci and the frequency of focus establishment. The model ignores population demography and assumes no restrictions on population growth. The result is a computationally simple model that predicts the rate of spread of a multiple-focus plant invasion. Although the data required to parameterise the model is potentially obtainable from remotely sensed time series of plant invasions, I know of no application of the model using real data.

Markov models

Markov models are a family of spatial models that use the tools of matrix algebra to formulate discrete-space and discrete-time models. These models are commonly used in forecasting landscape change (Baker 1989). In its simplest form the Markov model can be expressed as

$$\mathbf{n}_{t+1} = \mathbf{P}\mathbf{n}_t \qquad (5)$$

where $\mathbf{n}_t$ is a column vector, $\mathbf{n} = (n_t \ldots n_m)$, whose elements are the fraction of land area in each of m states at time t, and **P** is an m X m matrix, whose elements, p_{ij}, incorporate the birth, death, and change rates of each state during the time step from t to $t + 1$. The transition probabilities are usually derived from a sample of transitions occurring during some previous time interval.

The principle assumptions of Markov models are that the transition depends only on the current distribution of states (i.e. history has no effect), and that transition probabilities are stationary over time. When transition probabilities can be estimated from a remotely sensed time series of an invasion, Markov models are likely to be extremely useful. Although Markov models have been used to forecast changes in vegetation state (e.g. Hobbs 1983, Callaway and Davis 1993) and the spread of root disease epidemics (Chardoeuf et al. 1993), they have not been applied to plant invasions.

The spatial-phenomenological models do not invoke any ecological mechanism in the prediction of plant invasive spread. Consequently they have the advantage that they can forecast future events without making any ecological assumptions. This is particularly useful if one does not understand the ecological mechanisms involved and if one is confident that the past can be used to predict the future. The disadvantages of the phenomenological models are that one's understanding of ecological invasions and other ecological processes is not enhanced, the results cannot be applied to other invasion scenarios, and the techniques cannot be applied without historical spread records.

Spatial-mechanistic models

In contrast to the phenomenological models, mechanistic models are based on independent estimates of ecological parameters which are usually made at a lower hierarchical level. Since these ecological parameters represent some ecological processes, the predictions are a function of ecological interactions and the model's assumptions. Mechanistic spread models therefore use ecological assumptions regarding the spatial dynamics of invading populations to predict plant spread.

Reaction diffusion models

The first category of spatial-mechanistic models I consider are the reaction-diffusion models which use the formulation of partial differential equations (PDE). This formulation allows the modelling of population density in both space and time. The simplest invasion model of this type describes a homogenous population, which grows exponentially and spreads by random diffusion into a uniform environment, such that

$$\frac{\partial u}{\partial t} = ru + D\left(\frac{\partial^2 u}{\partial x^2} + \frac{\partial^2 u}{\partial y^2}\right) \qquad (6)$$

where $u(x,y,t)$ is the density of organisms at spatial co-ordinates x,y and at time t and D is the diffusivity or the rate of random movement of individuals in the population. The diffusivity is assumed to be normally distributed. Although D is a key parameter, it is seldom estimated from independent data sources (Williamson 1989, but see recent animal spread applications e.g. Andow et al. 1990, van den Bosch et al. 1992, Hengeveld 1994, Holmes 1993). Models of this type, first applied in an invasion scenario by Skellam (1951), produce waves of invaders whose asymptotic velocity approaches the square root of $4rD$ (Andow et al. 1990). Hence, the model predicts that the rate of spread is a simple function of the rate of population increase and the rate of movement of individuals in the population.

Reaction diffusion models have been successful in describing the range expansion of a number of animal species and diseases (Okubo 1980, Hengeveld 1989, Holmes et al. 1994 provide examples). However, Andow et al. (1990) noted that these models can underestimate rates of spread by an order of magnitude; they attributed this varied performance to the artefact of using parameters estimated at an inappropriate hierarchical level to project invasion rates at higher hierarchical levels.

Many criticisms have been levelled at the simplifying assumptions that reaction diffusion models make. For instance, Holmes (1993) criticised the assumption of simple random diffusion and proposed a model where diffusion is modelled as a correlated random walk. Her results, however, illustrated that the basic reaction diffusion model is satisfactory for the prediction of the rate of spread. Van den Bosch et al. (1992) and Hengeveld (1994) criticised the reaction diffusion model's inability to account for interactions between age, reproduction and movement. They present a number of approximation formulae, first applied to the spread of plant diseases

(van den Bosch et al. 1988), which allow these interactions to be incorporated into an estimation of the rate of spread. These modifications improved the model's performance, but not significantly so (van den Bosch et al. 1992, Hengeveld 1994).

Despite the moderate success of reaction diffusion models in describing animal invasions, few plant invasion models have used the reaction-diffusion approach. Skellam (1951) applied the model to the postglacial spread of oak trees in England. In this application, the model was useful only in that it identified that secondary dispersers such as rooks must have increased the diffusivity. In a similar application, Birks (1989) used published estimates of *r* and Holocene invasion rates to estimate the diffusivity of a number of tree species in the British Isles. The estimates of diffusivity resulting from this analysis were unrealistically high, suggesting that Holocene invasions were not the result of simple single focus expansions (Birks 1989).

The reaction diffusion model predicts that the square root of infestation area when plotted against time should give a straight line and that the slope should correspond to the mean rates of advance of an invasion front. These two predictions and a 6 year aerial photograph data set of the spread of *Mimosa pigra* into a northern Australian wetland were used as a test of the reaction diffusion model. Neither prediction was realised and it was concluded that this model was inadequate for modelling plant spread (Lonsdale 1993). However independent estimates of the rate of spread, the intrinsic rate of population growth (*r*) and diffusivity (*D*) for plant invasions are required before the adequacy of the reaction-diffusion model can be assessed in a plant invasion context (see Williamson 1989).

These plant invasion applications suggest that some of the fundamental assumptions of the reaction diffusion model are not valid in a plant spread context. The first, and perhaps most unacceptable assumption is that dispersal distances are normally distributed. Many wind- and animal dispersed plants have a strongly leptokurtic, and not normal, dispersal profiles (Howe and Wesley 1986). In addition, Allen et al. (1991) found that more than one mechanism of dispersal was required to account for the observed spread of *Opuntia imbricata* in a Texas, U.S.A. rangeland, and consequently suggested that more than one diffusion co-efficient may be required in diffusion based models of plant spread. Since the shape of the dispersal distribution is generally regarded as being more important than demographic parameters in influencing invasions (van den Bosch et al. 1992), these assumptions are worrying. Secondly, the assumption that an invasion can be represented as a single expanding focus is seldom met in plant invasions (Mack 1985, Moody and Mack 1988).

More general criticisms of the reaction diffusion models have been made. Since, the mathematics of PDE models are complicated, modifying the model is not simple; in particular, the incorporation of stochasticity is not easily achieved (Holmes et al. 1994). The incorporation of stochasticity is required for dealing with the effects of rare long distance dispersal events and Hengeveld (1994) attributed the model's occasional underestimation of spread rates to its inability to deal with these long distance dispersal events. Work on animal spread suggests that PDE models are likely to be unsuitable at scales where the variability in the rate of movement of individuals is high (Goldwasser et al. 1994), where dispersal is directed and not random, and where environmental heterogeneity influences the pattern of organism movement (Johnson et al. 1992). Hence, despite their success in a number of case studies, it is clear that the potential of reaction-diffusion models is limited.

All the spatial models discussed above do not explicitly reference space (i.e. by a co-ordinate system), nor do they consider (explicitly) the spatial heterogeneity of the environment. The use of spatially explicit models of plant spread is advocated in situations where: (1) spatial environmental heterogeneity influences population dynamics, particularly when the spatial arrangement of safe sites for alien colonisation is regarded as important; and (2) where neighbourhood interactions such as the presence and spatial arrangement of nascent foci influences the invasion pattern. I consider two types of spatially explicit models here: metapopulation models and individual-based cellular automata models. Both consider space and time as discrete variables and typically adopt a simulation approach.

Population dynamic metapopulation models

A metapopulation is a system of local populations connected by dispersing individuals (Hanski and Gilpin 1991). Thus a metapopulation model can be represented as a system of population models that describe the local population dynamics at each location. For exponential population growth, the growth of the *i*th population in a *n*-population system can be represented by the difference equation,

$$N_i(t+1) = N_i(t) r_i - \sum_{j=1}^{n} E_{ij} + \sum_{j=1}^{n} E_{ji} \qquad (7)$$

where n is the number of populations, N_i^t is the number of individuals in population i at time t, r_i^t is the intrinsic rate of population growth of population i at time t. E_{ij} is the number of individuals emigrating from population i to population j.

Although most metapopulation applications deal with the processes of extinction and establishment of new populations, the mathematical and theoretical tools provided by the metapopulation framework are likely to be useful in the development of invasion models. If one considers the *focus* of an invasion to be analogous to the *local population* of a metapopulation, then it becomes apparent that metapopulation research has much to offer when modelling invasions.

A metapopulation model of plant spread was developed by Auld and Coote (1980 1990). This model considered the spread of a wind-dispersed annual or perennial species in a two-dimensional landscape. The landscape is divided into discrete local population sites, each of which supports exponential population growth. A proportion of each local population is assumed to disperse to neighbouring sites and sites differ in their susceptibility to colonisation. The model has been reasonably successfully applied in the prediction of the spread of *Nassella trichotoma* (Auld and Coote 1981) and *Avena fatua* in eastern Australia (Auld and Coote 1990).

More complex plant-metapopulation models have recently been developed. For instance, Perry and Gonzalez-Andujar (1993) developed a metapopulation model in which annual plant metapopulations existed in a hexagonal array of cells. The model incorporated local population dynamics within each cell, driven by density dependent competition; dispersal from a parent cell declining exponentially with distance, and spatial and temporal environmental heterogeneity. Although this model was not developed as an invasion model, its application to an invasion scenario would not require much modification.

Individual-based cellular automata models

Metapopulation models divide the population into local populations, and consequently impose a patch structure on the model population. When this patch structure does not correspond to patterns of environmental heterogeneity experience by the modelled population, a scaling artefact is introduced (McCauley et al. 1993). It follows that individual-based (*sensu* Huston et al. 1988) cellular automata models are appropriate in situations where no ecological motivation for the delineation of local populations exists, when the environmental conditions experienced by

each individual plant is important, or when the presence of a single plant can influence invasion patterns. A general cellular automata model can be described as consisting of a discrete array of cells, each cell capable of taking on a finite number of states (0,1,...,*M*). To obtain the value of the i^{th} cell at time $t+1$ ($C_{t+1}(i)$) a transition rule is developed which depends on the previous state of the cell and the state of other cells in the array,

$$C_{t+1}(i) = F(C_s(i), C_s(j)) \qquad (8)$$

where $C_s(j)$ represents the states of other cells in the array denoted by the index j at earlier times when $s < t$ (Ermentrout and Edelstein-Keshet 1993). First developed in the 1940s (see Hogeweg 1988 for a historical account), cellular automata models are now widely used in plant ecological applications (e.g. Crawley and May 1987, Silvertown et al. 1992, Colasanti and Grime 1993). An advantage of these models is that a variety of data sources can be integrated (Wissel 1992b), including theoretical, empirical and anecdotal information. This information is translated into a set of transition rules that define the behaviour of the system. As is the case for metapopulation models, the incorporation of stochasticity and environmental heterogeneity is easily achieved in cellular automata models. Despite their obvious potential, I know of no individual-based cellular automata models of invasive plant spread.

SUMMARY: SELECTING A MODEL

Selecting which plant spread model is appropriate for a given invasion requires careful consideration of the ecology of the invasion (Figure 1). An understanding of the processes which determine and constrain the invasion is crucial for selecting an appropriate modelling approach, since the models available for forecasting invasion events make different assumptions regarding the ecology of plant spread (Table 2). In this section I summarise how the assumptions made about the ecology of plant spread and the study's objectives determine the most appropriate modelling technique.

Simple demographic models are suitable only when it can be assumed that the area invaded is related to population density, or when the objective is to estimate the chances that an invasive plant population will successfully establish. The type of demographic model selected depends on the nature of population growth; exponential models can be used to model populations whose growth is density independent and logistic models can be used to model density dependent growth; difference equations are useful for populations whose growth is

Table 2. The attributes of plant spread models (Y = yes, N = no, YN = yes or no, NA = not applicable)

Model type	Model attribute						
	Discrete time	Discrete space	Density dependent	Stochastic	Multiple foci	Spatially explicit	Individual based
Simple-demographic							
Exponential	N	NA	N	N	N	N	N
Logistic	N	NA	Y	N	N	N	N
Logistic difference	Y	NA	Y	N	N	N	N
Stochastic	Y	NA	YN	N	N	N	N
Spatial phenomenological							
Regression	YN	YN	NA	N	N	N	N
Geometric	N	N	NA	Y	Y	N	N
Markov	Y	Y	NA	Y	Y	N	N
Spatial-mechanistic							
Reaction-diffusion	N	N	YN	N	N	N	N
Metapopulation	Y	Y	YN	Y	Y	Y	N
Cellular automata	Y	Y	YN	YN	Y	Y	Y

characterised by discrete recruitment events or non-overlapping generations; stochastic models are advocated when population numbers are small and/or when variability in the system being investigated strongly influences population dynamics.

Empirical data demonstrates that the rate of increase of aerial cover of an invasive focus (ca. 0.03-0.1; see Williams et al. 1987, Perrins et al. 1993, Pysek and Prach 1993) is an order of magnitude lower than the intrinsic rate of increase of most plant populations (ca. 0.09-0.8; Silvertown et al. 1993). Hence simple demographic models are unlikely to provide accurate predictions of invasion rates. Although the nature of population growth undoubtedly influences rates and patterns of an invasion (Hengeveld 1994), translation of population increase into rates of spread clearly requires the incorporation of spatial movement patterns. Consequently, the value of demographic models lies in non-spatial invasion issues, for example the determination of the chances of establishment of an invasive plant population. In this context, invasion researchers can gain from the experience of conservation biologists concerned with minimum viable populations and risk assessment (see Burgman et al. 1993 for a review of appropriate models).

When the spatial component of the invasion, i.e. area invaded, is of concern, spatial models should be used. The spatial phenomenological models assume that the intricate ecological interactions of the invasion process are best summarised by empirically derived constants. These constants are estimated from historical data sources (e.g. floristic records or remotely sensed time series). Spatial-phenomenological models are advantageous when knowledge of the invasion mechanism is limited, or when quantitative data required for a mechanistic model is not available. Regression models establish a relationship between area invaded by an invasion focus

and time, and have been useful in quantifying invasion patterns. Although their predictive power is limited to repeat invasions, the comparative analysis of invasions using regression models can facilitate theory and model development.

The geometric model builds on the regression approach by providing the tools for the investigation of multiple focus invasions. The model has been extremely useful as a heuristic tool in illustrating the importance of nascent foci in promoting invasion rates. However, the geometric model requires the estimation of spread rates that take into account focus size and environmental heterogeneity. Unfortunately, because replicated empirical precedents for the estimation of these constants is unlikely to be realised in practice, parameterisation of the model is implausible. In addition, the model does not allow for the spatial interaction of invasion foci, for example overlapping foci and the establishment of daughter foci. These limitations suggest that, although the model has considerable value as a heuristic tool, its predictive value is limited.

Markov models are the last type of spatial phenomenological models considered. They offer the advantage over regression and geometric models in that multiple vegetation states (e.g. different invasive plant densities) can be modelled in discrete space and time. A second advantage is that methods for the estimation of state transition probabilities are well established. Their success in modelling the plant successional dynamics of a number of systems suggests that they have potential for forecasting future invasive plant densities. However, like all the spatial phenomenological models, Markov models require an empirical record and a confidence that the past can be used to predict the future.

Since the spatial-phenomenological models are underpinned by empirically derived constants, they cannot lead to the development of a predictive understanding (Levin 1989) of invasive plant spread. Furthermore, the pursuit of mechanistic models of plant spread is required for predicting spread in scenarios for which no empirical precedent exists. Reaction diffusion models represent a family of partial differential equation models that have been widely employed to describing animal invasions. They are best applied in single-focus invasion scenarios where the population dynamics are well described by continuous parameters, and where environmental heterogeneity and stochasticity are not important (Holmes et al. 1994). In many invasion scenarios, however, environmental heterogeneity and stochasticity are important components of an invasion (Mollison 1986). In addition, the use of the continuous parameters of population increase (r) and diffusion (D) represents a mathematical convenience that ignores the observation that environmental disturbance and heterogeneity are a common component of invasion systems. A

fundamental limitation of the partial differential equation models, however, is their technical complexity, which limits their use as building blocks for the construction of more realistic models (Vance 1984).

Metapopulation models and individual-based cellular automata models, by contrast, are discrete-space, discrete-time modelling approaches. Because these models adopt a simulation approach, they are flexible enough to allow the incorporation of spatial heterogeneity and stochasticity. Metapopulation models aggregate individuals into local populations and are therefore less computationally demanding than individual-based models. Metapopulation models are consequently the models of choice from a practical perspective. However, individual-based approaches are recommended in scenarios where the spatial structure of a metapopulation model does not correspond to patterns of environmental heterogeneity (McCauley 1993), when fine scale ecological heterogeneity is important, or when neighbourhood interactions (e.g. competition) are important. Both these models offer much potential for the development of predictive theories of alien plant spread. Successful implementation of the models will, however, require that considerable effort be devoted to parameterising the models. The observation that few estimates of the two reaction-diffusion parameters exist for any organisms (Williamson 1989) suggests that one should be cautious in advocating the use of parameter-rich spatial models (Doak and Mills 1994).

CONCLUSIONS

Very few attempts at modelling alien plant spread are reported in the literature, despite the devastating effects alien plants have had on natural ecosystems and the opportunities an invading population provides for testing ecological theory. This review illustrates that both knowledge and tools are available to predict rates and patterns of alien plant spread. Such predictions could facilitate the development of more effective strategies for alien plant management and will provide exciting opportunities for the development and testing of theories of population and community ecology.

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CHAPTER 3

THE ROLE OF PLANT-ENVIRONMENT INTERACTIONS AND MODEL STRUCTURE ON THE PREDICTED RATE AND PATTERN OF INVASIVE PLANT SPREAD

Abstract. Alien plants invade many ecosystems worldwide and often have substantial negative effects on ecosystem structure and functioning. Our ability to quantitatively predict these impacts is, in part, limited by the absence of suitable plant spread models and by inadequate parameter estimates for such models. This chapter explores the role of model, plant and environmental attributes on the predicted rates and patterns of spread of alien pine trees (*Pinus* spp) in the Cape fynbos of South Africa. A factorial experimental design is used to (1) compare the predictions of a simple reaction-diffusion model and a spatially explicit individual-based simulation model; (2) investigate the sensitivity of predicted rates and patterns of spread to parameter values; and (3) quantify the effects of the simulation model's spatial grain on its predictions. The results indicate that the spatial simulation model places greater emphasis on interactions between ecological processes than the reaction-diffusion model does. This ensures that the predictions of the two models differ substantially for some factor combinations. The most important factor in the model is dispersal ability. Fire frequency, fecundity and age of reproductive maturity are of secondary importance, while adult mortality has little effect on the model's predictions. The results also show that the simulation model's predictions are sensitive to the model's spatial grain. This suggests that simulation models, which use matrices as a spatial framework, should ensure that the spatial grain of the model is compatible with the spatial processes being modelled. I conclude that parameter estimation and model development must be integrated procedures. This will ensure that the model's structure is compatible with the biological processes being modelled. Failure to do so may result in spurious predictions.

Key words: *Pinus*, fynbos, alien, invasion, reaction-diffusion model, spatially explicit individual-based simulation model, sensitivity analysis, scale, scaling artefacts, factorial simulation experiment, plant life history attributes, disturbance.

INTRODUCTION

The spread of invasive alien plants threatens the structure and functioning of many ecosystems worldwide (Drake et al. 1989). Unfortunately, syntheses of knowledge on biological invasions (Groves and Burdon 1986, Macdonald et al. 1986, Mooney and Drake 1986, Drake et al. 1989, di Castri et al. 1990, Richardson et al. 1992) have failed to develop any predictive theories of alien invasions (Lodge 1993). Although some workers have begun developing empirical invasion models that predict which species will invade which environments (e.g. Richardson et al. 1990, Rejmanek and Richardson 1996), it remains that very little is known about the rates, spatial patterns and determinants of invasive plant spread (Macdonald 1993). The magnitude and nature of the impacts of alien plants on natural systems demands the development of a framework for predicting alien plant spread.

Predicting rates and patterns of alien plant spread requires, *inter alia*, the formalisation of the relationships between the input and output components of an invasion system, i.e. a model. Most invasion models use information on the plant and environmental attributes of the invasion system to predict rates and patterns of alien plant spread (Chapter 2). Reaction-diffusion (R-D) models are probably the most widely applied invasion models, and they have been successfully used to predict the rates of animal invasions (Levin 1992). Because R-D models use the formulation of a partial differential equation, they allow the incorporation of spatial and population processes into a single framework which is capable of predicting rates of invasion (Holmes et al. 1994). The basic assumptions of R-D models are that populations are large enough for stochastic effects not to be important and that, in the absence of reproduction, the abundance of organisms decreases exponentially around the point of release (Czaran and Bartha 1992, Holmes et al. 1994). In a homogenous environment, where population growth is density independent, the R-D model predicts that the asymptotic rate of spread, in one-dimension, can be described as,

$$V \approx \sqrt{4rD} \qquad (1)$$

where V is the asymptotic velocity of the invasion, r is the intrinsic rate of population growth, and D is the diffusivity (Andow et al. 1990). The use of r implies that population growth is modelled as a continuous process, and that the rate of population increase is not modelled as a function of the population's age structure or environmental heterogeneity. Similarly, the parameter D implies that dispersal is modelled as a continuous function that is independent of age or environmental heterogeneity.

The assumptions of R-D models prevent the explicit investigation of the interactions between plant attributes, environmental heterogeneity and stochasticity. Because plant-environment interactions and stochasticity strongly influence invasion rates and patterns, this limits the predictive ability of R-D models (Chapter 2). An additional implication of this limitation is that equation (1) only provides an estimate of the rate, and not the pattern of invasive spread. Many of the limitations of the R-D models have been addressed by modifying the basic R-D model (see Hengeveld 1994, Holmes et al. 1994, Shigesada et al. 1995). Unfortunately, because the complexity of a R-D model increases with increasing realism, many of these modified R-D models are either special cases, or are analytically intractable. Since the historical rationale behind pursuing the R-D approach in an invasion context was the promise of an analytical solution, it is clear that alternate model formulations should be investigated. Such an alternative must integrate space, ecological processes and stochasticity into a single predictive framework. Spatially explicit simulation models meet these criteria (Vance 1984, Huston et al. 1988, Czaran and Bartha 1992, Chapter 2) and have been applied in plant invasion scenarios (e.g. Auld and Coote 1980, 1990) and spatial problems in ecology in general (e.g. Wiener 1981, Vance 1984, Silvertown et al. 1992). Another advantage of spatially explicit models is that the spatial locations of individual modelling elements are traced. This ensures that context-specific aspects of individual plant behaviour can be simulated (Czaran and Bartha 1992) and that the model's predictions can be geographically referenced and hence linked to Geographical Information Systems for further analyses. It appears, however, that no attempt has been made to compare the performance of a R-D model with spatially explicit simulation models. Such a comparison will allow the evaluation of model performance, and this is the first objective of this paper.

To achieve this objective, I built a spatially explicit, individual-based simulation (SEIBS) model of alien plant spread. The SEIBS model is constructed to simulate the spread of alien pine trees from established commercial plantations into natural fynbos ecosystems, since this is a major management problem in the mountain catchments of the fynbos biome, South Africa (Richardson et al. 1992). The literature on pine invasions in fynbos suggests that five factors (adult fecundity; dispersal ability; time to reproductive maturity; the temporal frequency of post-fire recruitment opportunities; and fire survival of adults) are major determinants of spread (Richardson et al. 1990, Richardson and Cowling 1992). The SEIBS model is constructed so that each of these factors can be explicitly modelled. This means that the direct effects and interactive effects of each of these factors on the rates and patterns of

pine tree spread can be determined. It follows that the second objective of this paper is to investigate how rates and patterns of plant spread are influenced by these five factors, with the aim of improving the understanding of invasion processes.

Investigating the model's sensitivity to these five factors addresses two additional and important issues. Firstly, as is often the case with ecological systems, empirical data for parameter estimation are not available (Okubo 1980, Crawley 1983, Williamson 1989). The SEIBS model's output will be useful for setting priorities for empirical data collection. Secondly, an analysis of the model's response to different factors and factor levels acts as a sensitivity analysis. Although not always included in simulation studies, sensitivity analyses are imperative for defining the range of conditions for which a simulation model's predictions hold (Caswell and John 1992, Fahrig 1991). Spatially explicit simulation models are also sensitive to the model's spatial grain. However, it appears that few process-based simulation models have explored the importance of this spatial artefact (Costanza and Maxwell 1994); it is therefore the third objective of this paper to investigate the importance of this artefact. It should be noted that since R-D models use continuous parameters, they do not suffer from this limitation; as a consequence they can, and have been, applied over a range of spatial scales (Hengeveld 1994).

The objectives of this paper are to: (1) compare the qualitative and quantitative behaviour of the simple R-D model (equation 1) with that of a spatially explicit individual-based simulation (SEIBS) model; (2) explore the effects, interactions and hence the importance of two ecologically realistic levels of five factors (adult fecundity, dispersal distribution, age of reproductive maturity, fire return interval, and fire survival) on the rate and pattern of spread of pine trees in a homogenous landscape; and (3) investigate the sensitivity of the SEIBS model's predictions to the spatial grain of the individual modelling elements.

METHODS

Description of the spatially explicit individual-based simulation model and the 2^5 factorial simulation experiment

A 2^5 factorial experimental design (Table 1) was used to investigate the effects of fire survival (FS), adult fecundity (AF), age of reproductive maturity (ARM), mean dispersal distance (MDD) and fire return interval (FRI) on the rate and pattern of alien plant spread. A factorial design was used since it is a very efficient way of examining multi-factor experiments and detecting interactions (Montgomery 1984). The SEIBS model considers a two-dimensional grid (150x400) of sites. Although using a larger grid would be more realistic, computer time limitations prohibited this. Each site is of equal environmental quality, represents a spatial area of 100 m^2 (the approximate canopy area of an adult pine tree), and can be occupied by one plant. A number of assumptions are made about the behaviour of pine trees in these sites:

(1) Time passes in discrete intervals of 1 year.

(2) Fire is a source of environmental heterogeneity. Two fire return intervals (factor FRI) are considered, an 8-year and 25-year return interval. These two fire regimes are within the extremes (4 - 45 years) reported for fynbos systems (van Wilgen 1987). A fire covers the entire modelling landscape; i.e. the spatial heterogeneity of fires is not considered. Burning the entire modelling landscape is consistent with the observed spatial extent of fires in fynbos (Kruger and Bigalke, 1984).

(3) Recruitment is only possible following fires. This assumption is supported by the fact that most invasive pines in fynbos are serotinous (Richardson et al. 1992), and that fire provides recruitment opportunities by removing the understorey (Bond et al. 1984, Richardson et al. 1992).

(4) Only adult trees are able to reproduce and two scenarios are considered, with adulthood and hence age of reproductive maturity (factor ARM) being reached at either 6 or 15 years after recruitment. This is consistent with the range of age of reproductive maturity observed in invasive pine trees in fynbos (Richardson et al. 1992).

Table 1: Factor levels and combinations used in the 2^5 factorial simulation experiment, and reaction-diffusion model parameter estimates.

Factor combination	Factors*					R-D+	
	FS	AF	MDD	ARM	FRI	λ	*D*
1	0.4	100	70	6	8	1.586	390
2	0.1	100	70	6	8	1.574	390
3	0.4	10	70	6	8	1.196	390
4	0.1	10	70	6	8	1.179	390
5	0.4	100	20	6	8	1.586	31.8
6	0.1	100	20	6	8	1.574	31.8
7	0.4	10	20	6	8	1.196	31.8
8	0.1	10	20	6	8	1.179	31.8
9	0.4	100	70	15	8	1.168	390
10	0.1	100	70	15	8	1.159	390
11	0.4	10	70	15	8	1.043	390
12	0.1	10	70	15	8	1.029	390
13	0.4	100	20	15	8	1.678	31.8
14	0.1	100	20	15	8	1.159	31.8
15	0.4	10	20	15	8	1.043	31.8
16	0.1	10	20	15	8	1.029	31.8
17	0.4	100	70	6	25	1.465	125
18	0.1	100	70	6	25	1.460	125
19	0.4	10	70	6	25	1.144	125
20	0.1	10	70	6	25	1.137	125
21	0.4	100	20	6	25	1.465	10.2
22	0.1	100	20	6	25	1.460	10.2
23	0.4	10	20	6	25	1.144	10.2
24	0.1	10	20	6	25	1.137	10.2
25	0.4	100	70	15	25	1.187	125
26	0.1	100	70	15	25	1.183	125
27	0.4	10	70	15	25	1.068	125
28	0.1	10	70	15	25	1.063	125
29	0.4	100	20	15	25	1.187	10.2
30	0.1	100	20	15	25	1.184	10.2
31	0.4	10	20	15	25	1.068	10.2
32	0.1	10	20	15	25	1.063	10.2

* FS = Fire survival (probability); AF = Adult fecundity (recruits); MDD = Mean dispersal distance (m); ARM = Age of reproductive maturity (yrs); FRI = Fire return interval (yrs); + λ =Finite rate of population increase; D = Diffusivity (m^2/yr).

(5) Fire causes mortality and adult mortality is less than juvenile mortality. Anecdotal observations suggest that fire-induced mortality of juvenile pine trees is extremely high (Richardson 1988). Consequently, I set the probability of juvenile fire survival at 0.05 for all simulations. Since fire-induced adult mortality varies with bark thickness (McCune 1988), two probabilities of adult fire survival (factor FS), 0.4 and 0.1, are defined. The model assumes that mortality occurs during fires, i.e. no inter-fire mortality is considered. Individual mortality occurs when a computer-generated uniform random number is greater than the probability of fire survival for that tree. Adult trees killed in a fire are able to contribute recruits to the next generation, but the space they occupied becomes available for colonisation.

(6) Two levels of adult fecundity (factor AF), 10 and 100 recruits per adult plant are considered. Although empirical data on the fecundity of invading pines is poor, the 10 - 100 range is in agreement with published accounts of pine invasions in fynbos (van Wilgen and Siegfried 1986, Richardson 1988).

(7) The spatial position of a recruit is determined by the position and dispersal ability of the parent plant. It is assumed that the chance of recruitment decreases as a negative exponential function of distance from the parent plant. This is a reasonable assumption, if we accept that: (i) dispersal is a negative exponential function of distance from the parent plant, as is reported in many empirical studies (see Harper 1977, Okubo and Levin 1989 for reviews); (ii) there is a homogeneous spatial distribution of recruitment opportunities for pine trees in fynbos (Richardson et al. 1992); (iii) no secondary dispersal and post dispersal predation occurs. Using these assumptions, empirical data (van Wilgen and Siegfried 1986, Benkman 1995) and a wind dispersal model (Greene and Johnson 1989) as calibration, I define the dispersal profile of a heavy-seeded pine species as following a negative exponential distribution with a mean dispersal distance (factor MDD) of 20 m. Similarly, I assume that the dispersal profile for a small-seeded pine would follow a negative exponential distribution with a mean dispersal distance of 70 m. The model's dispersal algorithm involves generating a negative exponential random number (with a mean of 20 m or 70 m, as is appropriate) to determine the distance of each recruit from the parent plant and a uniform random number (in the range 0-360°) to determine the dispersal direction of each recruit. Dispersal distances are truncated at a distance of 1 km from the parent plant. The distance and direction of each recruitment event is converted to grid co-ordinates, and successful recruitment only occurs if the grid location is unoccupied. This means that pre-emptive competition (sensu Schoener 1983) for sites

occurs, and that an individual can only be displaced through mortality (cf. assumption 5).

Replicated (n = 10) simulation runs of a 2^5 factorial experimental design (Table 1) were performed, resulting in a total of 320 simulation runs. Replicates were performed to record the variance in model performance caused by the stochastic elements in the dispersal and mortality rules (cf. assumptions 5 and 7). Each simulation run was initiated with a row of mature trees along a *Y* dimension edge of the 150x400 cell grid (Figure 1). This row of trees represents the edge of a commercial pine tree plantation. All runs were terminated when a single tree reached the *Y* dimension edge opposite the site of initiation or after 1000 simulation years. The *X* dimension edges were wrapped; this removes boundary effects (Gardner et al. 1987). The following response variables were measured from each simulation run:

(1) Rate of spread (m/yr), estimated by simple linear regression of the maximum distance of the invasion front from the site of initiation (as defined in Figure 1) against simulation time.

(2) The mean and standard deviation of plant density within an invasion focus, expressed as areal cover per area of invasion focus.

(3) The mean and standard deviation of perimeter length of the invasive front, expressed as perimeter length per linear length of invasion front in meters.

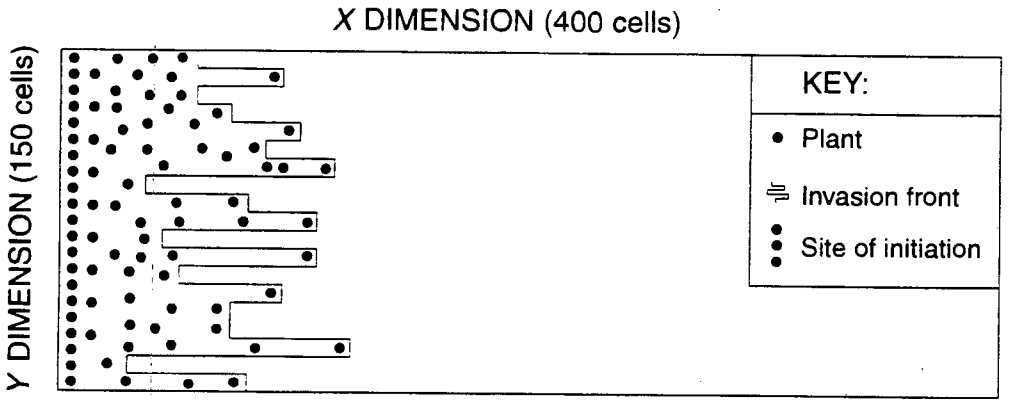

Figure 1. Diagram illustrating the spatially explicit, individual-based modelling environment.

Parameterising the reaction-diffusion model

I used the structure and assumptions of the simulation model to construct a life table and population projection matrix for each factor combination. These matrices were used to estimate, using the power method (Caswell 1989), the finite rate of increase (λ) for each factor combination (Table 1). For example, for factor combination 1 a projection matrix with 6 classes (=ARM) is constructed. Since only the sixth class can reproduce and reproduction can only occur after fires, the annual reproduction of the sixth class is 12.5 (AF/FRI). Mortality occurs during fires and hence for classes 1-5 only 0.88125 (FRI-1/juvenile fire survival) of the population moves into the next class. Similarly the proportion of class six surviving annually is 0.925 (FRI-1/FS). Diffusivity (D, m^2/yr) was also estimated from the structure and assumptions of the simulation model for each factor combination, using the formula provided by Andow et al. (1990). For factor combination 1 the diffusivity is 390 m^2/yr ($2MDD^2\pi^{-1}FRI^{-1}$). This procedure mimics the sampling of a real population over time, by summarising the underlying determinants of the population's vital rates in two parameters, λ and D. By substituting r for $\ln(\lambda)$, equation (1) was used to calculate the R-D model's predicted rate of spread.

Spatially explicit individual-based simulation model: spatial grain simulation experiment

To explore the effects of spatial grain on aspects of the SEIBS model's performance, simulations of alien plant spread were run at different spatial grains. The mean of the two levels of each factor used in the 2^5 factorial simulation experiment was used to parameterise the runs. Replicated (n = 10) simulations were performed for seven spatial grains (10 m^2; 20 m^2; 40 m^2; 80 m^2; 160 m^2; 320 m^2; 640 m^2). Increasing the spatial grain in this manner introduces a conceptual modification into the model's structure, since one no longer models individual plants of size of 10 m^2 areal cover, but rather individual patches of vegetation of various sizes. The extent of the model was maintained at 150x400 cells in order to avoid any boundary-related artefacts. Apart from these modifications, the scale-dependent simulation runs had the same structure and assumptions as the 2^5 simulation runs.

RESULTS

Reaction-diffusion model versus spatially explicit individual-based simulation model

The mean (n = 10) rate of spread for each factor combination of the SEIBS model was compared to the R-D model's estimate (Figs 2A and 2B). The two models produced very similar median estimates of spread rate, although the SEIBS model produced a wider range of estimates (range 0 - 44 versus 1.6 - 26.8 m/yr). Comparison of the model's rate of spread estimates for each factor combination (Figure 3) revealed that neither model consistently over- nor under-estimated spread rates, suggesting that the patterns observed were not due to parameter estimation errors. The SEIBS model provided a higher estimate of spread rate for factor combinations 1 to 8, lower estimates for combinations 9 to 16, similar estimates for combinations 17 to 24, and higher estimates for combinations 25 to 32 (Figure 3). Hence the models differed both qualitatively and quantitatively in behaviour.

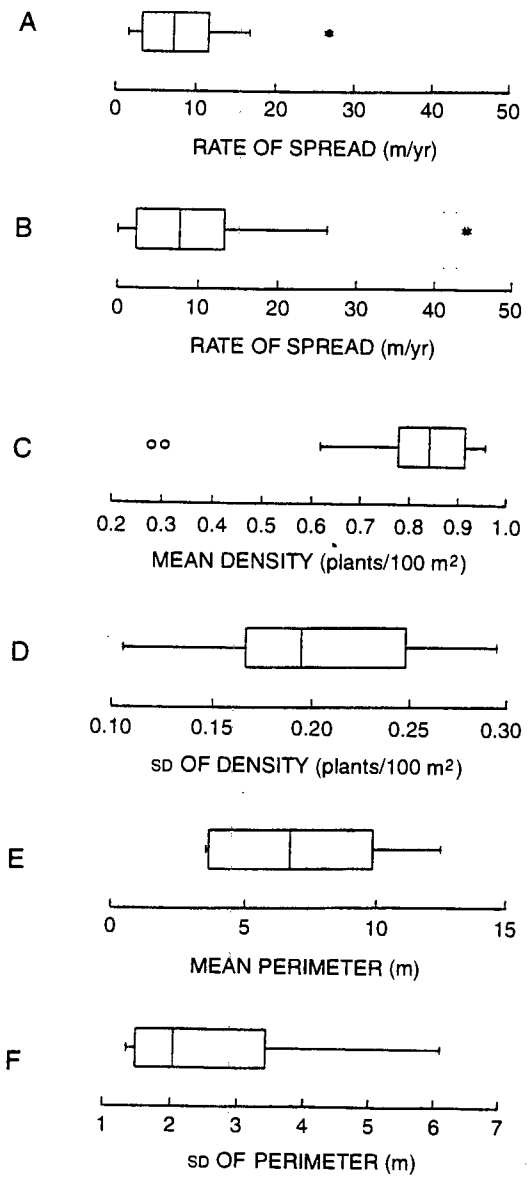

Figure 2. Box and whisker plots of the range of responses for 32 factor combinations (Table 1) of the reaction-diffusion model rate of spread (A), spatially explicit individual-based simulation (SEIBS) model rate of spread (B), SEIBS model mean density of plants in invasion focus (C), SEIBS model standard deviation of plants in invasion focus (D), SEIBS model perimeter length (E), and SEIBS model standard deviation of perimeter (F). SEIBS responses are the mean of replicated simulations (n = 10).

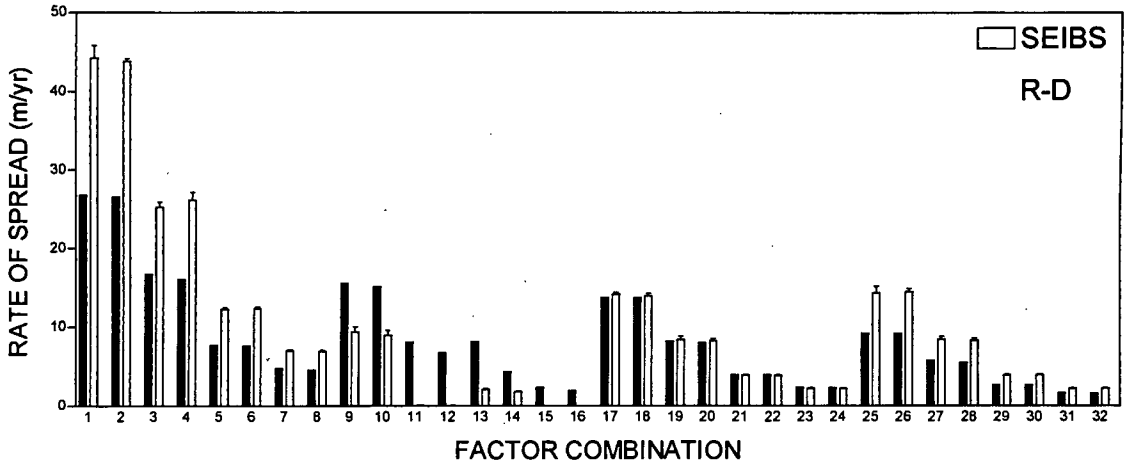

Figure 3. Comparison of the rate of spread predicted by the reaction-diffusion (R-D) and spatially explicit individual-based simulation (SEIBS) models for each of 32 factor combinations (Table 1). SEIBS values are mean ± 1 SD (n = 10).

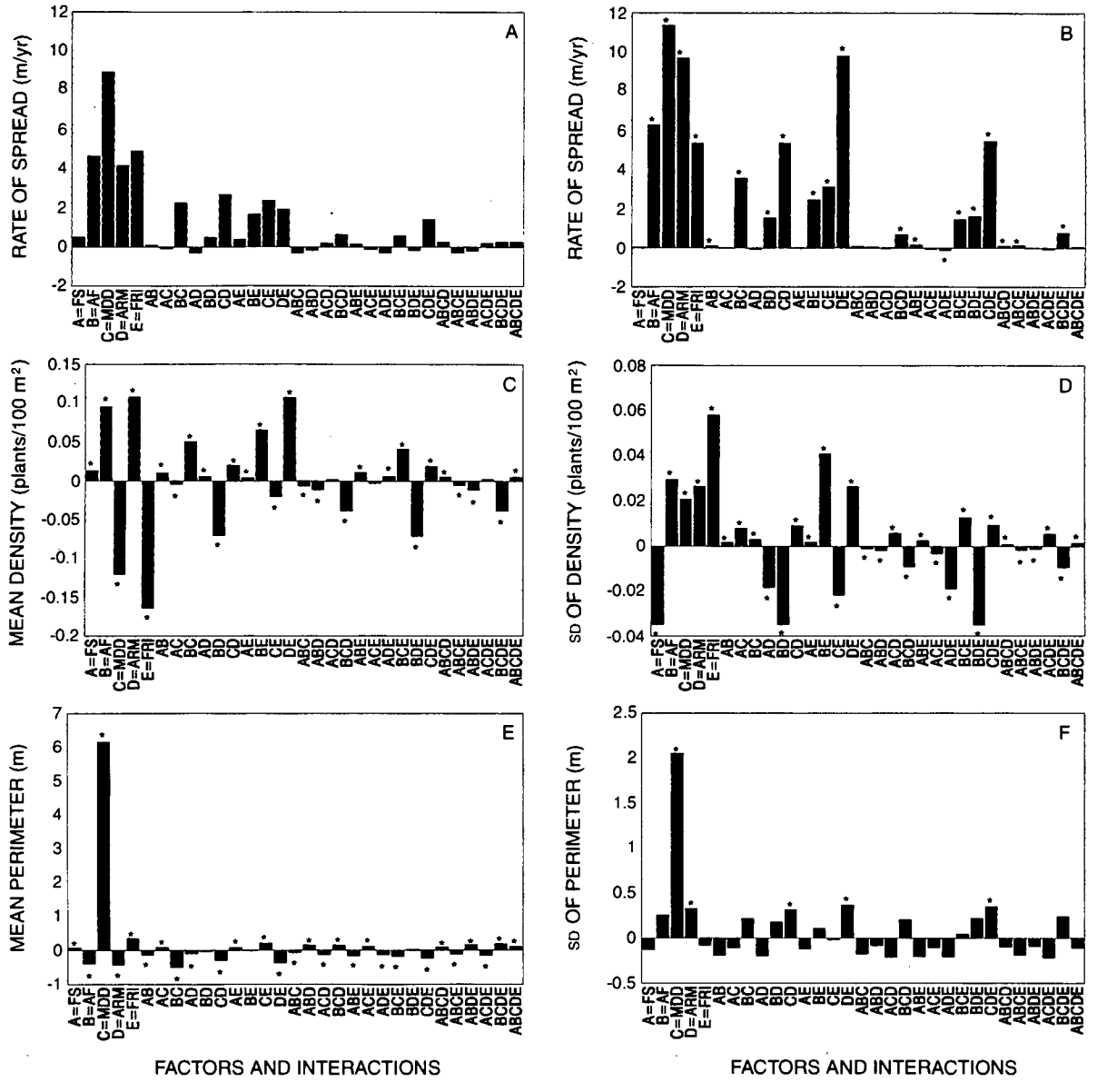

Figure 4. The mean effect of each factor and interaction on the reaction-diffusion model rate of spread (A), spatially explicit individual-based simulation (SEIBS) model rate of spread (B), SEIBS model mean density of plants in invasion focus (C), SEIBS model standard deviation of plants in invasion focus (D), SEIBS model perimeter length (E), and SEIBS model standard deviation of perimeter (F). FS:= Fire survival; AF:= Adult fecundity; MDD:= Mean dispersal distance; ARM:= Age of reproductive maturity; FRI:= Fire return interval. * Indicates significant effects ($p < 0.05$).

The main effects and primary interactions of the factors on the predicted rate of spread for these two models (Figure 4A and 4B) illustrated a number of similarities and differences. The models were similar in that they both highlight the primary importance of all factors except fire survival. In addition, both models indicated the importance of interactions between the factors in determining the rate of spread. The quantitative details of the importance of the different factors on spread rate did differ between the models; in particular the SEIBS model emphasised the importance of a short time to reproductive maturity (high level ARM). The magnitude of the primary interactions between the factors illustrated more differences between the models. Large interactions, similar in magnitude to the main effects, were detected by the SEIBS model (e.g. ARM x FRI, ARM x MDD and ARM x FRI x MDD), but not by the R-D model.

The 2^5 factorial simulation experiment

The box and whisker plots describe the range of responses the SEIBS model produced (Figs 2B-2F). The rate of spread was right skewed and ranged from 0 to 44 m/yr (Figure 2B). The mean density within an invasion focus was left skewed (range 0.28 to 0.96; Figure 2C) and the standard deviation density was normally distributed (range 0.11 - 0.29; Figure 2D). The mean perimeter was weakly left skewed (range 3.5 - 10.2 m; Figure 4E); while the standard deviation perimeter was strongly left skewed (range 1.3 - 6.1 m; Figure 4F).

A number of strong correlations between the SEIBS response variables were detected (Table 2). Spread rate was significantly correlated with the standard deviation of plant density within the invasion front, and the mean and standard deviation of perimeter length of the invasion front. A strong correlation was detected between the related measures, mean perimeter length of the invasion front and standard deviation of the length of the invasion front. A negative correlation between mean density of plants within an invasion front and the mean length of the perimeter of the invasion front was also detected. The standard deviation of density and the standard deviation of perimeter length were positively correlated. All other correlations were weak.

The box and whisker plots and effects plots (Figs 2B and 4B) illustrated that higher levels of all factors resulted in an increased rate of spread. The FS levels chosen for this study did not have a significant effect on the spread rate, and the primary interactions involving FS were not large in magnitude (Figure 4B). High levels of MDD and ARM resulted in 115 and 98 %

Table 2. Pearson correlation coefficients between the response variables of the spatially explicit, individual-based simulation model and means and standard deviations of the response variables for the 320 simulation runs of the factorial experiment.

Response Variable	Rate of spread	Mean density	SD density	Mean perimeter	SD perimeter	Mean	SD
Rate of spread	1					9.848[a]	10.99[a]
Mean density	0.104	1				0.808[b]	0.157[b]
SD density	0.510	0.161	1			0.202[b]	0.058[b]
Mean perimeter	0.417	-0.506	0.137	1		6.765[c]	3.143[c]
SD perimeter	0.483	-0.142	0.166	0.562	1	2.488[c]	1.734[c]

[a] m/yr; [b] plants/100 m^2, [c] m.

increases in the mean spread rate respectively. High levels of AF and FRI, while of less importance, increased the mean spread rate by 63 and 54 % respectively. Two of the primary interactions (MDD x ARM; ARM x FRI) were of a similar magnitude to the main effects, and they resulted in 54 and 99 %

respective increases in the mean spread rate, while the secondary interaction between MDD, ARM and FRI had a large effect on spread rate (55 % increase).

The mean density of plants in the invasion focus responded to all five factors, and many primary interactions were large in magnitude (Figure 4C). High levels of FRI and MDD reduced mean density by 20 and 15 % respectively, while high levels of ARM, AF and FS increased mean density by 13, 11 and 2 % respectively. Four of the primary interactions (ARM x FRI, AF x ARM, AF x FRI, AF x MDD) were of a similar magnitude to the main effects, influencing mean density by between 2 and 13 %. Two secondary interactions (AF x ARM x FRI and AF x MDD x FRI) were of large magnitude; the first reduced mean density by 9% and the second increased mean density by 5 %.

The standard deviation of plant density within the invasion focus did not produce the same pattern as mean density (Figs 4C and 4D). High FS reduced the standard deviation of density by 17 %, while high levels of AF, MDD, ARM and FRI led to increased variations in density (15, 10, 13 and 29 % respectively). Five primary interactions were of a similar magnitude to the main effects. The FS x ARM, AF x ARM and MDD x FRI interactions led to decreases in the standard deviation of density of 9, 17 and 11 % respectively. Increases in standard deviation in density were caused by the AF x FRI and ARM x FRI interactions (respective

increases of 20 and 13 %). Two large secondary interactions (FS x ARM x FRI and AF x ARM x FRI) decreased standard deviation density by 9 and 17 % respectively.

The mean length of perimeter and standard deviation of perimeter (Figs 4E and 4F) illustrated the same trends; namely that MDD was the primary determinant of the perimeter length of the invasion focus. This was not surprising, considering the strong positive correlations between these two related measures of invasion pattern (Table 2). The high level of MDD resulted in a 91 % increase in the mean perimeter length and an 82 % increase the standard deviation of perimeter length. All other factors and interactions had substantially smaller effects on perimeter length.

Scaling artefacts and the spatially explicit individual-based model

The correlation matrix revealed that all the correlations between the model's response variables over a range of spatial grains were statistically significant (Table 3). Rate of spread was negatively correlated with mean density and positively correlated with standard deviation density, mean perimeter and standard deviation perimeter. Mean density was negatively correlated with standard deviation density, mean perimeter and standard deviation perimeter; while standard deviation density was positively correlated with mean and standard deviation perimeter. Mean and standard deviation perimeter were strongly correlated.

The SEIBS model's predictions were not consistent over a range of spatial grains. None of the observed spatial grain trends were smooth, although this is probably because changing spatial grain in this study also changed the scale at which measurements were made and rounded off the location of a recruit to the nearest cell. The predicted rate of spread was relatively stable over a spatial grain from 10 m^2 to 160 m^2, with only a 12.4 % decrease in the predicted rate of spread observed (Figure 5A). Further increase in the spatial grain resulted in substantial decreases in the predicted rate of spread. The mean density of patches within the invasion focus increased rapidly with increasing spatial grain (Figure 5B). The standard deviation of patch density within the invasion focus decreased slowly with spatial grain in the range 10 m^2 to 320 m^2, after which it decreased dramatically (Figure 5C). The mean perimeter length and standard deviation of perimeter length both exhibited a rapid decline with spatial grain that levelled out at 80 m^2 (Figs 5D and 5E).

Table 3. Pearson correlation coefficients between the response variables of the spatially explicit, individual-based simulation model and means and standard deviations of the response variables for the 70 scale-dependent simulation runs.

Response Variable	Rate of spread	Mean density	SD density	Mean perimeter	SD perimeter	Mean	SD
Rate of spread	1					9.122[a]	3.861[a]
Mean density	-0.743	1				0.945[b]	0.029[b]
SD density	0.983	-0.745	1			0.155[b]	0.050[b]
Mean perimeter	0.525	-0.948	0.509	1		2.797[c]	1.784[c]
SD perimeter	0.405	-0.903	0.392	0.982	1	1.396[c]	0.451[c]

[a] m/yr; [b] plants/100 m^2, [c] m.

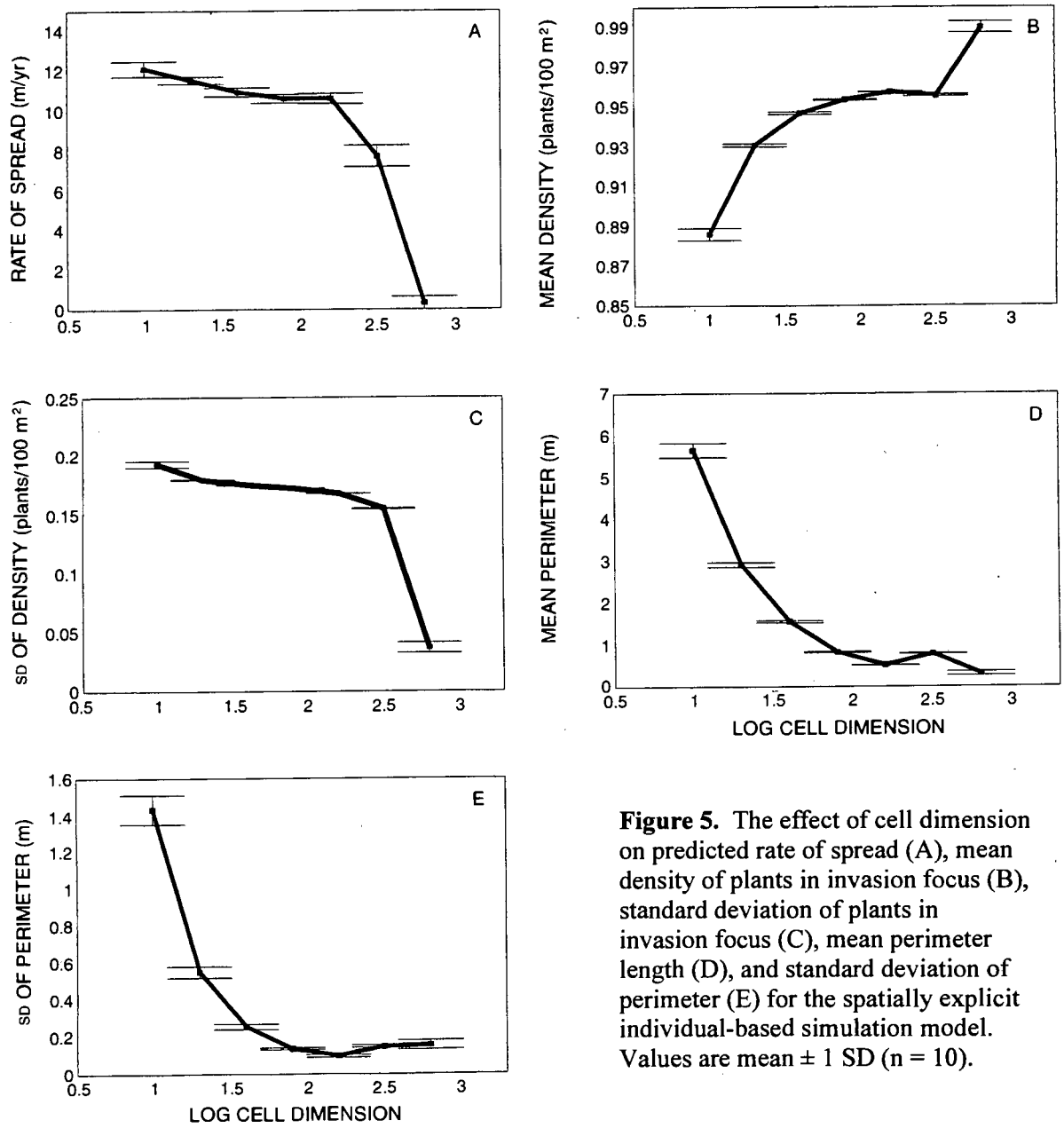

Figure 5. The effect of cell dimension on predicted rate of spread (A), mean density of plants in invasion focus (B), standard deviation of plants in invasion focus (C), mean perimeter length (D), and standard deviation of perimeter (E) for the spatially explicit individual-based simulation model. Values are mean ± 1 SD (n = 10).

DISCUSSION

Reaction-diffusion versus spatially explicit individual-based model

The range of predictions made by the R-D and SEIBS models falls within the lower range of spread rates reported in the literature for invading plant species (see Chapters 5 and 6) and for Holocene tree spread rates (see Chapter 5). The utility of this comparison is limited since there are few published estimates of rates of spread and since the taxa, environments and methodologies reported in the literature are likely to yield different spread rates (Chapters 2, 5 and 6). The R-D and SEIBS models differ in the range of spread rate predictions they make and in the predicted effects of plant life history attributes and disturbance frequency. These differences can be attributed to the R-D model's use of two continuous parameters to summarise plant-environment interactions. This chapter showed that the use of spatially explicit model formulations and continuous parameters, which summarise many ecological processes into a few parameters, can qualitatively and quantitatively influences a model's predictions. This is well illustrated by the large interaction between age of reproductive maturity and mean dispersal distance in the SEIBS model, where stands of a slow-maturing, short-dispersing species spread slower than would be predicted from a knowledge of their mean dispersal distance and age of reproductive maturity alone. This interaction occurs because slow-maturing, short-dispersing species are unlikely to have many adult trees on the edge of an invasion focus when recruitment opportunities occur. Hence, although the R-D model recognises that invasive success is a function of both the reproductive and dispersal potential of individuals (Skellam 1951), the SEIBS model illustrates that an explicit knowledge of the effects and interactions of factors that influence reproductive potential (indexed by r in the R-D model) is required for predicting spread rates. A number of workers have recognised limitations of the R-D approach and this has motivated the modification of the basic R-D model. It seems that these attempts were in vain, firstly because these modifications have not substantially influenced model predictions (e.g. Holmes 1993, Hengeveld 1994), and secondly since these results suggest that these limitations are inherent in the structure of R-D models.

The larger effects of the factor mean dispersal distance in the SEIBS model indicates that the use of a stochastic dispersal rule results in higher predicted spread rates, implying that the incorporation of stochastic rules can substantially modify a model's predictions for small populations. The same result was found by Goldwasser et al. (1994). Furthermore, the tails

of dispersal profiles of wind-dispersed species may not tail off in a negative exponential manner, but may decrease more gently (Portnoy and Wilson 1993, Greene and Johnson 1995). In such circumstances, an alternative dispersal algorithm to the one used here will be needed. These rarer long-distance events can result in the formation of new disjunct invasion foci, which can substantially increase the observed rate of spread as well as change the pattern of spread (Moody and Mack 1988, Shigesada et al. 1995). Since the incorporation of alternative dispersal distributions into the SEIBS model would be technically simple, it follows that effort should be devoted to collecting data on the tails of dispersal profiles (see Chapter 5).

Determinants of invasive spread

The SEIBS model quantifies the more rapid invasion of plants with shorter juvenile periods; higher fecundity, longer dispersal distances and which grow in more frequently disturbed environments. Importantly, the model quantifies the effects on rate of spread of the interactions between these factors. This study, therefore, allows for the quantification of how different suites of life history and environmental attributes influence the chance of invasion. This is a progression from previous studies, which merely identified the attributes of invasive plants (e.g. Richardson et al. 1990, Lodge 1993, Rejmanek and Richardson 1995); this is developed further in Chapter 4). The large magnitude of the interactions between factors means that all factors, except fire survival, can strongly influence spread rates. The consequence of this is that for most invasion scenarios in fynbos, effort should be placed on obtaining good empirical data for all factors except fire survival.

The SEIBS model predicts that high levels of adult fire survival, high adult fecundity, short dispersal distances, short time to reproductive maturity and infrequent fires all lead to increased mean stand density. Predictions of alien plant abundance may be useful for predicting the impacts of alien plants in situations where alien abundance is correlated with alien plant impacts (e.g. Richardson et al. 1989). The plant-environmental traits, identified by the SEIBS model, which increase local density differ from the traits that influence the rate of plant spread. This observation is supported by the poor correlation between rate of spread and stand density (Table 2).

Mean and standard deviation of alien plant density were influenced by some complex interactions; this further emphasises the utility of the SEIBS approach. For example, while

fecund individuals that mature quickly on average resulted in denser and more variable stand densities, the interaction between these two factors decreased the mean and standard deviation of stand density. This decrease can be attributed to the reduced availability of establishment sites around parent plants caused by density-dependent effects associated with pre-emptive competition for establishment sites. Any model that does not consider real co-ordinate space is unlikely to account for this reduction in safe site density (Perry and Gonzalez-Andujar 1993). The interactions between fire frequency, reproductive age and adult fecundity provide another example of the importance of interactions for predicting stand density: for slow-maturing plant populations that produce few offspring, a short fire return interval leads to high levels of mortality, but this same fire return interval provides recruitment opportunities for a fast-maturing and fecund population.

Spatial grain and the spatially explicit individual-based simulation model

The SEIBS model's predictions for all response variables were strongly influenced, both quantitatively and qualitatively, by changes in spatial grain. The most sensitive variables were mean plant density and perimeter length, whereas predicted rate of spread and variation in plant density were less sensitive to small changes in spatial grain, yet very sensitive to large changes in spatial grain. Since the strength and sign of the correlations between response variables of the scale-dependent simulation runs (Table 3) and the factorial simulation runs (Table 2) differ substantially, I conclude that the correlations identified in the factorial runs are not stable over different spatial grains, and conversely that the trends identified in the scale-dependent runs are a function of the parameter values selected. This can be illustrated by considering that since increasing spatial grain increases the distance a recruit must travel to leave its parent cell, a species with a short dispersal distance will be more sensitive to increased spatial grain (Fahrig and Paloheimo 1988; Gardner et al. 1991). These results provide firm evidence that simulation models that use matrices as a spatial framework need to ensure that the spatial grain of the model is compatible with the spatial processes being modelled. This is supported by recent criticisms that spatial metapopulation models often have spatial structures that are inappropriate for the ecological processes being modelled (McCauley et al. 1993). Such inconsistencies may substantially influence predictability, and I consequently recommend that the robustness of spatial models' predictions to changing spatial grain be routinely evaluated as part of sensitivity analysis procedures. The spatial grain of environmental heterogeneity is a related factor, which should also influence the selection of the most appropriate spatial grain for a spatial simulation

model. This is because environmental heterogeneity can strongly influence invasion dynamics (Bergelson et al. 1993), and the spatial grain of the model must be such that it is capable of representing the patterns of environmental heterogeneity which influence the organism's response (Kotliar and Wiens 1990).

CONCLUSIONS

This study illustrates that reaction-diffusion models are inadequate building blocks for the modelling of spatial phenomena, a conclusion supported by Vance (1984) but not by Hengeveld (1994). In particular, this paper demonstrates that the reaction-diffusion model's failure to mimic ecological processes and interactions between these processes decreases the model's predictive ability. A spatially explicit individual-based simulation model demonstrated the importance of such interactions. The importance of interactions between ecological factors and the lack of empirical data on these factors suggests that considerable effort should be devoted to empirical data collection. It should be noted that the high rates of increase (λ) typical of invasive plants means that invasive plants may be expected to display chaotic dynamics; in such cases even the best data will not generate reliable predictions. The simulation model described here and the results of this study provide clear objectives for such empirical work. On a cautionary note, it was shown that spatial scaling artefacts influence the performance of grid-based spatial simulation models. This suggests that model development requires knowledge of not just the ecological processes of importance, but also of the spatial scale of these processes. In essence this means that the parameter estimation and model development processes must be tightly integrated.

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PINE INVASIONS IN THE SOUTHERN HEMISPHERE: MODELLING INTERACTIONS BETWEEN ORGANISM, ENVIRONMENT AND DISTURBANCE

Abstract. Current theories of plant invasion have been criticised for their limited heuristic and predictive value. I explore the heuristic and predictive potential of a model which explicitly simulates the mechanisms of plant invasion. The model, a spatially explicit individual-based simulation, is applied to the invasion of pine trees (*Pinus* spp., Pinaceae) in three vegetation types in the southern hemisphere. The model simulates factors that have been invoked as major determinants of invasive success: plant traits, environmental features and disturbance level. Results show that interactions between these determinants of invasive success are at least as important as the main effects. The complexity of invasions has promoted the belief that many factors must be invoked to explain invasions. This study shows that by incorporating interactions and mechanisms into models we can potentially reduce the number of factors needed to predict plant invasions. The importance of interactions, however, means that predictions about invasions must be context-specific. The search for all-encompassing rules for invasions is therefore futile. The model presented here is of heuristic value since it improves our understanding of invasions, and of management value since it defines the data and models needed for predicting invasions.

Key words: *Pinus*, disturbance, life-history attributes, environment-type, interactions, spatially explicit individual-based model, invasion theory, biological invasions

INTRODUCTION

There are at least three good reasons for pursuing a predictive understanding of the ecology of alien plant invasions. A predictive understanding can (1) increase our ability to mitigate the negative economic and environmental impacts of invasions (e.g. Higgins et al. 1997), (2) challenge our assumptions concerning the factors that control plant distribution and abundance (Harper 1977, Mack 1985, Richardson and Bond 1991, Lodge 1993a), and (3) provide techniques for predicting rates of species range changes in response to climate change (Bond and Richardson 1990, Lodge 1993b, Thompson 1994, Chapter 2).

Research stimulated by the SCOPE program on biological invasions explicitly sought to identify the attributes that allow some organisms to invade and the features that make some environments more susceptible to invasions (Drake et al. 1989). However, it has been suggested that it is unrealistic to expect general rules for predicting which organism will invade which environment to emerge (e.g. Crawley 1987, Gilpin 1990, Lodge 1993a, Vermeij 1996). It is argued that the complexity of the interactions between alien plants, the native biota and the environment they invade precludes prediction (Roy 1990, DeFarrari and Naiman 1994, Pysek and Pysek 1995, Thompson et al. 1995, Burke and Grime 1996). Certainly, existing theoretical models of invasion typically cannot handle such complexities and have not been of much heuristic or predictive value (Crawley 1987, Gilpin 1990, Lodge 1993a). It follows that invasion researchers are facing a dilemma: they must either abandon hopes for a mechanistic theory of plant invasions in favour of exclusively statistical models (Gilpin 1990, e.g. Burke and Grime 1996, Crawley et al. 1996, Rejmanek and Richardson 1996, Williamson 1996), or explore the potential of models which explicitly incorporate the ecological mechanisms of plant invasions in building a theory of plant invasions. In exploring such mechanistic models one can control the sources of variation in the system and, thus, assess the main and interactive effects of different factors in determining whether an organism can invade. Although such models lie in the uneasy territory between general and realistic models (Levins 1966), this territory must be explored before we accept that statistical models are our only predictive tools.

Three observations on alien plant invasions influenced the approach adopted here. First, the population size of an invasive plant must be able to increase from a small founder population. Second, interactions between plants and disturbance (both natural and human-mediated) are key processes in many invasions. Third, invasions are spatial processes. These observations suggest that a plant invasion model should simulate the spatial and temporal dynamics of small populations as influenced by spatial and temporal patterns of disturbance. The model I develop meets these criteria by borrowing concepts from existing plant succession and plant population models: the model simulates the population dynamics of individual plants (e.g. Pacala and Silander 1985) whose behaviour is defined by their life history attributes (e.g. Noble and Slatyer 1980, Huston and Smith 1987) in a spatially-explicit environment (e.g. Pacala and Silander 1985). The model is structured around results of numerous studies of the dynamics of invasions of pine trees (*Pinus* spp., Pinaceae) into forests, shrublands and grasslands of the southern hemisphere (reviewed by Richardson and Higgins 1998). This allowed the comparison of the model's output with documented pine invasions. Data available on these invasions are, however, not sufficient to fully parameterise the model. This is because many factors implicated

however, not sufficient to fully parameterise the model. This is because many factors implicated in invasions are often only correlated with the ecological mechanism; it follows that data needed are not clearly defined, never mind collected.

The aim of this chapter is to develop a simulation model of the complex dynamics of alien plant invasions. I hope that the model will have value as: (1) a heuristic tool for improving the understanding and management of plant invasions; and (2) a guide to the data requirements for predictive models of plant invasions.

THE CASE STUDY: PINE INVASIONS IN THE SOUTHERN HEMISPHERE

Species of pine trees (*Pinus* spp.) have been planted in a wide range of landscapes outside their natural range (Le Maitre 1998). This has created a series of transplant experiments with superb opportunities for studying invasions (Richardson and Bond 1991). Recent studies of these global transplants have used correlative techniques to identify the determinants of invasive success in pines (Richardson et al. 1990, Richardson et al. 1994, Rejmanek and Richardson 1996, Richardson and Higgins 1998). Key plant and environmental attributes which have been implicated in facilitating pine invasions in the southern hemisphere are: low seed-wing loading; small seed mass; short juvenile periods; high degree of serotiny; low fire tolerance; short intervals between large seed crops; intermediate disturbance frequency; high latitudes; long residence times; and a large extent of human planting. The challenge in building a mechanistic model is to translate these factors into operational functions. I do this for three types of environments which are regularly invaded by pines in the southern hemisphere (Richardson and Bond 1991) and for two of the functional groups of pines described by Keeley and Zedler (1998).

The environments are a fire-prone shrubland (e.g. fynbos shrubland: Cowling et al. 1997), a grassland (e.g. montane grassland: O'Connor and Bredenkamp 1997) and a temperate forest (e.g. afromontane forest: Midgley et al. 1997). These environments are defined in terms of the natural disturbance regime and hence the invasion opportunities and barriers they provide pine trees. Fires are the most important disturbances in shrubland and grassland (Bond and van Wilgen 1996). Treefalls are the major disturbance in temperate forests (Runkle 1985). Humans are increasingly modifying natural disturbance regimes. Many case studies have shown that human-induced disturbances make ecosystems more open to invasion (Fox and Fox 1986, Hobbs and Huenneke 1992). The most common human impact in southern hemisphere

shrublands has been an increase in ignition events; this increases fire frequency, decreases fire intensity, and increases the patchiness of fires (van Wilgen et al. 1990, Enright et al. 1996, Bond and van Wilgen 1996). Domestic livestock grazing, a common human-mediated impact in grasslands, can reduce plant biomass and thereby lead to less intense and patchier fires (Teague and Smit 1992, Bond and van Wilgen 1996). Commercial logging is the most common human disturbance in forests.

The two pine types investigated here were selected from the five pine life-history types described by Keeley and Zedler (1998). I chose these two pine types because they include most of the common invasive pines of the southern hemisphere (Richardson and Higgins 1998). The first pine type (Keeley and Zedler's "R-pine", e.g. *Pinus radiata*) is typical of landscapes characterised by predictable stand-replacing fires. The second pine type (Keeley and Zedler's "U-pine" e.g. *Pinus strobus*) occurs in habitats with unpredictable stand-replacing fires. Species of the R-pine type have: canopy-stored seeds which are released in response to fire (serotiny); short juvenile periods; thin bark (low probability of surviving a fire); seedlings which cannot tolerate shade; and annual cone production. Although many R-pine species can resprout (Keeley and Zedler 1998), I do not consider resprouting here. Species of the U-pine type are: not serotinous; have slightly longer juvenile periods; have thicker bark than the R-pines and the ability to self-prune (this confers on adults of this type a higher probability of fire survival); have shade tolerant seedlings; and have more infrequent cone production than the R-pine (they are mast seeders). Both pine types produce light and hence relatively dispersible seeds.

THE INVASION MODEL AND THE SIMULATION EXPERIMENT

The model is a development of the spatially explicit, individual-based simulation (SEIBS) model described in Chapter 3. I use this model to simulate the invasion of individuals of the two pine types into the three environment types, subject to five levels of human-mediated disturbance. The effects of the factors PLANT, ENVIRONMENT and DISTURBANCE, and their interactions on the predicted rate and pattern of invasion (Appendix 1) were quantified using an ANOVA of a complete factorial experimental design. Replicated simulations ($n = 20$) were run to allow the effects of the stochastic variables in the model to be quantified. Preliminary model runs showed that 20 replicates were enough to estimate the variance due to stochastic variables in the model.

The model description is divided into two sections. I first motivate the assumptions that underlie the model and then describe how these assumptions constitute the plant invasion model (Figure 1).

Model assumptions

Modelling environment

1. The model environment is a two dimensional grid of 100 x 200 sites. Each site was 10x10 m; this size was selected because: (1) the canopy area of adult pine trees can approach this size; and (2) neighbour interference becomes unimportant at this scale for pines (Kenkel 1988) and can therefore be ignored.
2. Each site is of initially equal environmental quality, but this may change during the simulation
3. Time passes in discrete annual units; it follows that vegetation age and tree age increase annually.
4. The model is initiated with a plantation of pine trees which occupy a 10x100 block of sites on the edge of the simulation environment. Hence the invasion is initiated from a relatively large founder population of adult trees which grow in a benign environment (suitable climate and protected from the natural disturbance regime). This simulates a situation where the propagule pressure is high; this is not the case in all invasion situations.

Disturbance and mortality

1. Two types of disturbance are considered: fire (in shrubland and grassland) and gap creation (in forest). These disturbance types are functionally equivalent in that they create opportunities for plant recruitment and potentially kill plants.
2. The model assumes that the frequency of fire ignition events in grassland and shrubland can be described by a sigmoidally shaped probability distribution and that fires occur more frequently in natural grasslands (typically every two years; Appendix 1) than in natural shrublands (typically every 20 years; Appendix 1). These assumptions and the selected return interval of ignitions for grasslands and shrublands are based on empirical data reported in van Wilgen et al. (1990). It is assumed that , under natural conditions, 1% of the forest is disturbed annually by treefalls (Runkle 1985). The spatial distribution of treefalls is assumed to be random, although larger trees are more likely to fall (Runkle 1985). A treefall is taken to affect one 10 x 10 m cell; this

reasoning is based on the small size of gaps reported in afromontane forests (Midgley et al. 1995). It is also assumed that alien and indigenous trees have the same probability of falling.

3. Fire spread is simulated as a spatially explicit process. The fire spread algorithm is a simple version of that advocated by Turner and Romme (1994), where fire spreads across the simulation landscape if neighbouring cells are combustible. It is assumed that grasslands and shrublands differ in their ages of combustibility. Hence a fire spread threshold (in practice a vegetation-age threshold) must be exceeded for a fire to spread (Appendix 1). These thresholds are based on the reported fire-return intervals of shrublands and grasslands (van Wilgen et al. 1990).

4. In forest, the probability of tree mortality in a disturbed site is 1 since the disturbance is tree-felling (Appendix 1). In grasslands and shrublands the probability of mortality for a tree in a burnt site depends on tree age and the level (intensity) of disturbance (Appendix 1). The shapes of these mortality curves are based on anecdotal and empirical accounts of pine tree mortality patterns (e.g. Richardson 1988, Richardson and Cowling 1994, Keeley and Zedler 1998, Chapter 6)

5. Human activities change the parameters of the prevailing disturbance regime. The most important human-mediated disturbance of grasslands is grazing (see above). It is assumed that grazing has no direct impact on pine invasions, but that it affects invasions indirectly through its effect on fire behaviour. Increased grazing intensity leads to more patchy fires by increasing the fire-spread threshold and reduces fire intensity (van Wilgen et al. 1990) and hence the probability of disturbance-induced tree mortality (Bond and van Wilgen 1996, Appendix 1). Humans affect shrublands by increasing fire ignitions (see above). These more frequent fires are likely to be less intense (van Wilgen et al. 1990) and it follows that the probability of disturbance-induced tree mortality decreases as the fire frequency increases (Bond and van Wilgen 1996, Appendix 1). Although these trends have been documented, data for quantifying these changes are poor. Consequently, the parameterisation of human-mediated disturbance covers a large range of possible ignition probabilities, fire-spread thresholds and disturbance-induced tree mortalities (Appendix 1). Treefelling is the most important human disturbance of forests. The model assumes that the pattern of forest tree felling is systematic, the first vegetation patch of suitable age (older than 20 years) encountered is cleared and this is repeated until the tree-felling quota is met. Like the fire disturbance levels, the levels of felling covers a large range of the possible values.

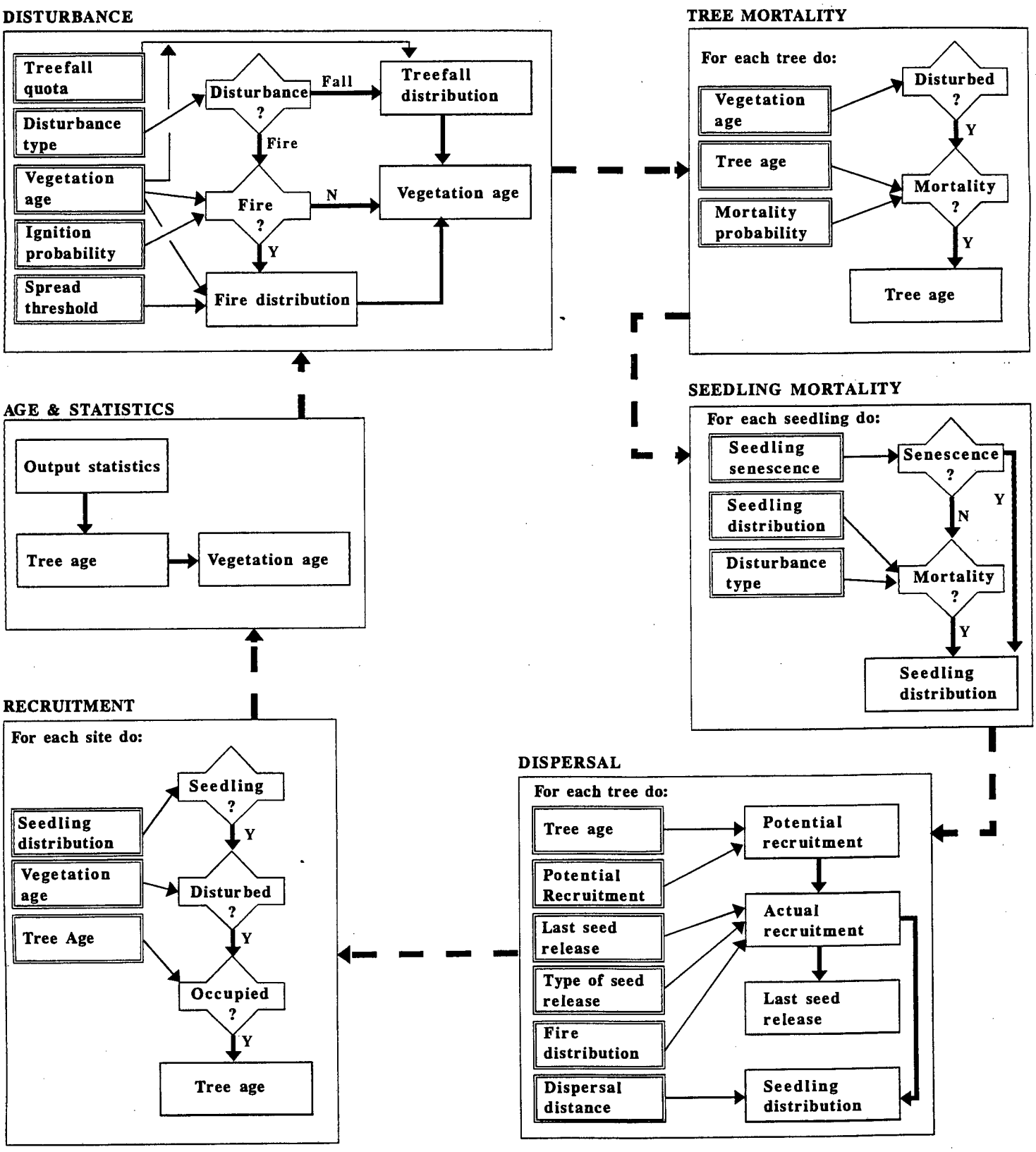

Figure 1. Flow diagram of a mechanistic model for simulating pine invasions in thesouthern hemisphere. Each block represents a program procedure. Dashed lines represent program flow from procedure to procedure, bold lines represent program flow within procedures and thin lines represent lines of influence. Blocks with a double border represent input variables. Single border blocks indicate dynamic variables that are being updated. Diamond shaped blocks control program flow by evaluating model rules.

Dispersal, seedling dynamics and recruitment

1. The recruitment capacity of a tree increases as a sigmoidal function of age (Appendix 1). The shape of this function is based on the assumption that a tree has no recruitment capacity until it reaches reproductive maturity, after which it rapidly approaches its maximum recruitment capacity (e.g. Enright et al. 1996). The observed age of reproductive maturity of pine trees (Richardson et al. 1990) and the estimated recruitment capacity of mature *Pinus pinaster* in fynbos shrublands (see Chapter 6) were used to calibrate these functions (Appendix 1).
2. A tree's actual recruitment depends on when it last released a large seed load. Trees are assumed to build up their seed load and release it when stimulated. This build-up of recruitment potential follows a sigmoidal pattern (e.g. Enright et al. 1996), and takes four years. A R-pine tree is stimulated to release its recruitment capacity when its site is burnt (see above). If no fire occurs, the R-pine releases 10% of its recruitment potential; this is consistent with a strongly serotinous pine type (Richardson et al. 1990). The U-pine is a mast seeder and releases its entire recruitment capacity during mast years, which occur roughly every six years (Keeley and Zedler 1998). Ten percent of its seed reserves are released in non-mast years; this is consistent with the coefficients of variation observed in mast-seeding species (Kelly 1994, Keeley and Zedler 1998).
3. Wind is the only dispersal vector considered (the pine types in this study are not adapted to animal dispersal). This ignores the few pine invasions which have been facilitated by fortuitous vertebrate dispersal vectors (e.g. *Pinus pinea* in South Africa: Richardson et al. 1990). It is assumed that dispersal distances can be described by a negative exponential distribution. Available data on pine trees (e.g. van Wilgen and Siegfried 1986, Lanner 1998) and other species (Harper 1977, Okubo and Levin 1989, Willson 1993) support this, although alternative dispersal models have been proposed (Allen et al. 1991, Portnoy and Willson 1993, Ribbens et al. 1994, Greene and Johnston 1995, see Chapter 5). A mean dispersal distance of 60 m is used for both pine types; this agrees with available data (van Wilgen and Siegfried 1986).
4. No directionality in wind dispersal is assumed.
5. Seedlings in unoccupied and disturbed sites recruit, i.e. the model assumes gap recruitment. The R-pine seedlings die if they fail to find a gap, whereas the U-pine seedlings only die if they are burnt (Keeley and Zedler 1998). These recruitment rules assume that the invasive trees are not directly influenced by indigenous plant species.

Model implementation

Initiating the model

The program is initiated by simulating the disturbance regime for 100 years, thus allowing a distribution of vegetation ages characteristic of the disturbance regime to develop before the simulation of the invasion. The "release" of the invasive plants is done by setting up a plantation of adult trees (10 x 100 sites) adjacent to a block of natural vegetation.

Disturbance

Disturbance is the first model procedure implemented during each simulation year (Figure 1). If the type of disturbance is fire, then the probability of ignition is calculated for a randomly located site (Appendix 1). If a uniform random number is less than this probability then a fire is ignited. A fire can spread from a burning core-cell to a neighbouring cell (4 nearest neighbours only) if the vegetation age of the neighbouring cell exceeds the spread threshold. The spread threshold is a normally distributed random number, with mean and standard deviation as defined in Appendix 1. When the fire has finished spreading, the burnt cells are assigned a vegetation age of zero (Figure 1). If the type of disturbance is a treefall, the model simulates natural and human-induced treefalls (Figure 1, Appendix 1). Natural treefalls are simulated as a Poisson process, constrained to vegetation patches over 20 years. Treefelling by humans is also constrained to vegetation patches over 20 years, but human treefellers work systematically through the simulation landscape clearing until the treefelling quota (Appendix 1) is met. The vegetation age of felled sites are set to zero (Figure 1).

Mortality

Tree mortality is only possible if a site is disturbed. The tree age and the mortality probability function (Appendix 1) are used to calculate a tree's probability of mortality. Mortality occurs if the probability of mortality is less than a uniform random number. Tree age is set to zero if mortality occurs (Figure 1). Seedling mortality occurs if seedlings are shade intolerant (Appendix 1). For shade tolerant seedlings, mortality occurs if the seedling's site is disturbed by fire (Figure 1). The seedling distribution is then updated to reflect the seedling mortality (Figure 1).

Dispersal

The dispersal procedure first calculates a tree's potential recruitment capacity, which is based on the tree's age and the recruitment function (Figure 1, Appendix 1). Actual recruitment is then calculated as a function of the recruitment capacity, the time since last seed release and the type of seed release (mast seeding or serotinous, Appendix 1). For the serotinous type (R-pine) a tree's entire recruitment potential is released if the tree's site was burnt; 10% of the recruitment potential is released if a tree's site is not burnt. The mast seeding type (U-pine) will release all its accumulated recruitment potential if the probability of a mast year is less than a uniformly distributed random number; if not, it releases 10% of its recruitment potential. The release of a large seed load resets the time since last seed release for both the R- and U-pine to zero. The actual recruitment potential is then dispersed. The distance of each seedling from each parent plant is determined by a negative exponential random number with a mean equal to the dispersal distance (60 m). A uniform random number in the 0-360° range determines the direction of each seedling from the parent plant. The distance and direction are then used to calculate the position of each seedling in the seedling distribution (Figure 1).

Recruitment

Recruitment occurs if a seedling is in a disturbed and unoccupied site (Figure 1). If recruitment occurs, the tree age distribution is updated to reflect this (Figure 1).

Age and statistics

This procedure first stores data for the calculation of the statistics and then updates the tree age and vegetation age to reflect the end of the simulation year (Figure 1). Three statistics were recorded from the model each year: (1) the simulation year; (2) the number of pine trees; and (3) the box dimension. The box dimension is the slope of a log-log least-squares linear regression of the number of boxes with sides of size h needed to cover the plant's distribution versus h (Maurer 1994). The box dimension is small for complicated and dispersed patterns, but approaches a value of 2 for solid patterns with smooth boundaries. Higher box dimensions

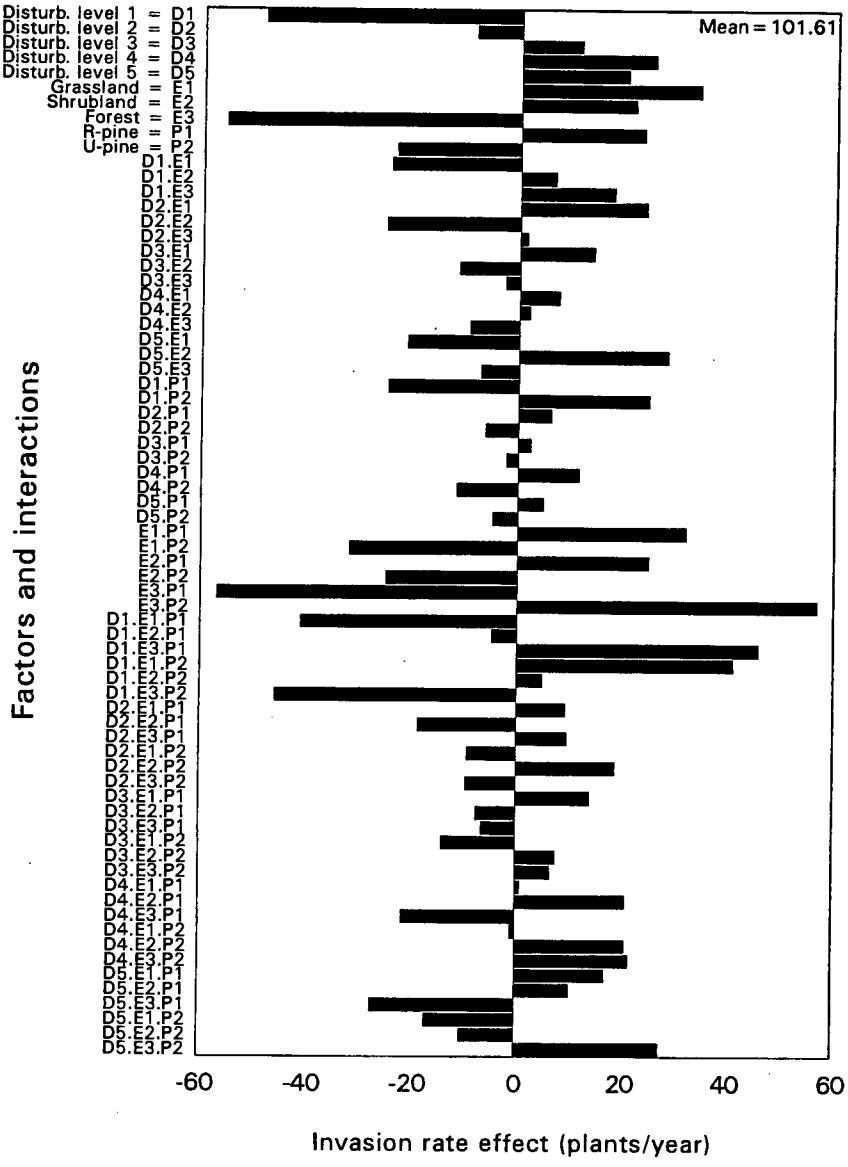

Figure 2. The main and interactive effects of disturbance level (D1-D5, as defined in Appendix 1), environment type (E1=grassland, E2=shrubland, E3=forest) and plant type (P1= R-pine, P2= U-pine; *sensu* Keeley and Zedler 1998) on the mean rate of invasion (102 plants/yr). Effects were estimated using ANOVA on 20 replicate runs of the full factorial experimental design (Appendix 1).

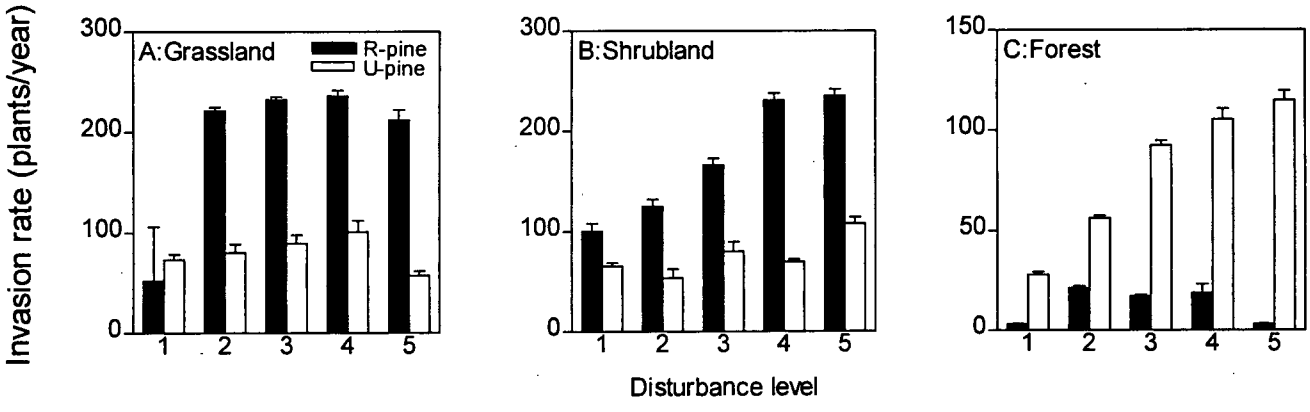

Figure 3. Mean and standard deviation (n=20) of predicted invasion rates for the R-pine and U-pine (*sensu* Keeley and Zedler 1998) under 5 levels of disturbance and in three environments (A=grassland, B=shrubland, C=forest).

would suggest that the invasion is proceeding as a uniform front, whereas lower box dimensions would indicate a scattered, disjunct invasion pattern. These data were then used at the end of the simulation run (100 years) to calculate: (1) the plant invasion rate, which is calculated as the slope of a least squares linear regression of plant number versus time; and (2) the average box dimension. These response variables were then
analysed in a full factorial analysis of variance (factors DISTURBANCE, ENVIRONMENT and PLANT, Appendix 1).

RESULTS

Invasion rate

A full factorial analysis of variance revealed that all factors and all orders of interactions significantly influenced the rate of invasion. The effects plot (Figure 2) shows the size of the main effects and interactions: many of the interactions have a greater effect than the main effects do. It is therefore not appropriate to generalise about which of the main effects is most important. The R-pine was more invasive than the U-pine in grassland and shrubland (Figure 3A, 3B). In forest, however, the U-pine was a faster invader (Figure 3C). This suggests that: the benefits of serotiny outweighed the costs of lower adult mortality (R-pine) in the fire-prone environments; and that mast seeding and persistent seedling banks (U-pine) are beneficial in forest. The shrubland and grassland were the most easily invaded environments under unmodified disturbance regimes, whereas unmodified forest showed the highest resistance to invasion (disturbance level 1, Figure 3). Higher levels of disturbance generally increased the invadability of all environments (Figure 3), although forest was less invadable under all levels of disturbance. The two pine types differed substantially in their responses to disturbance (Figure 3). The R-pine invaded grassland and shrubland rapidly, and forest slowly; its invasiveness increased linearly with disturbance in fynbos, asymptotically in grassland and unimodally in forest. The U-pine showed a less spectacular, but more consistent, ability to invade under all conditions. Natural forest was the environment type most resistant to U-pine invasion. Invasiveness of the U-pine increased linearly with disturbance in forest and responded unimodally to disturbance in grassland. Disturbance of shrubland did not influence the invasion rate of the U-pine.

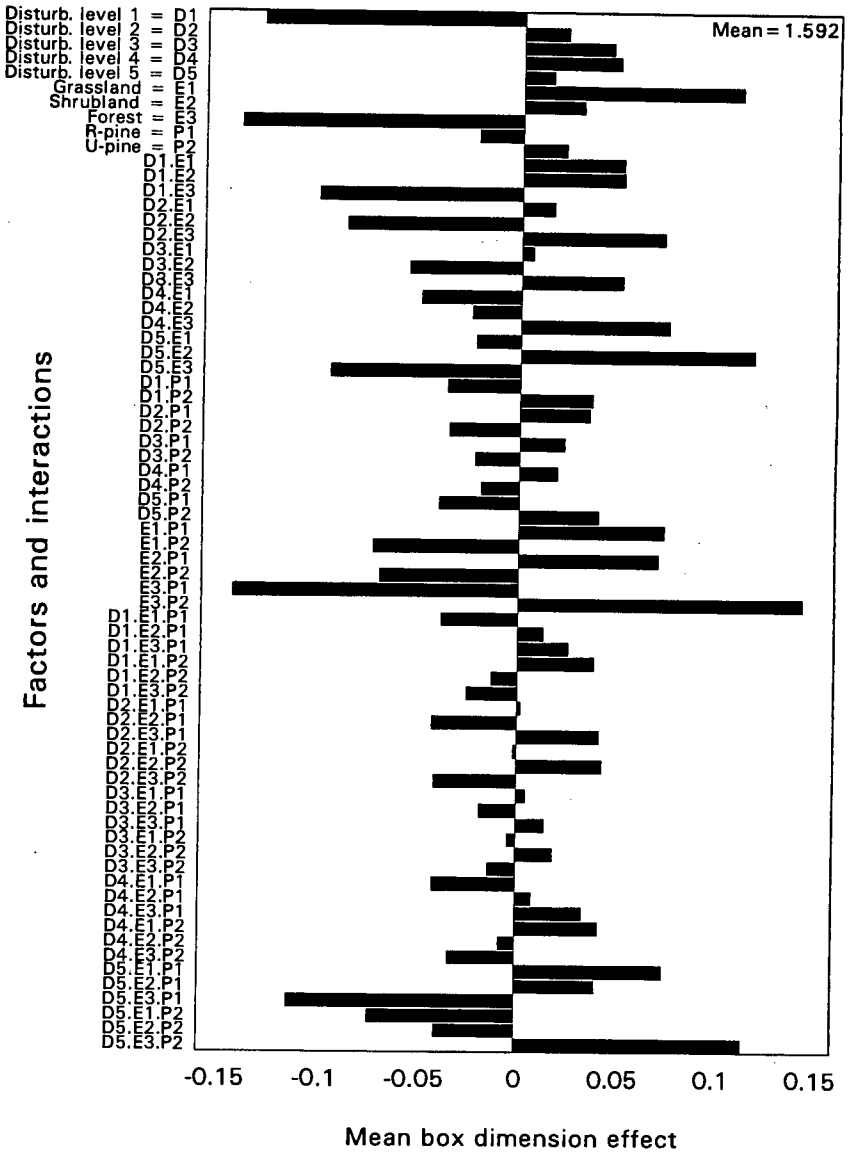

Figure 4. The main and interactive effects of disturbance level (D1-D5, as defined in Appendix 1), environment type (E1=grassland, E2=shrubland, E3=forest) and plant type (P1= R-pine, P2= U-pine, *sensu* Keeley and Zedler 1998) on the mean box dimension (1.592). Effects were estimated using ANOVA on 20 replicate runs of the full factorial experimental design (Appendix 1).

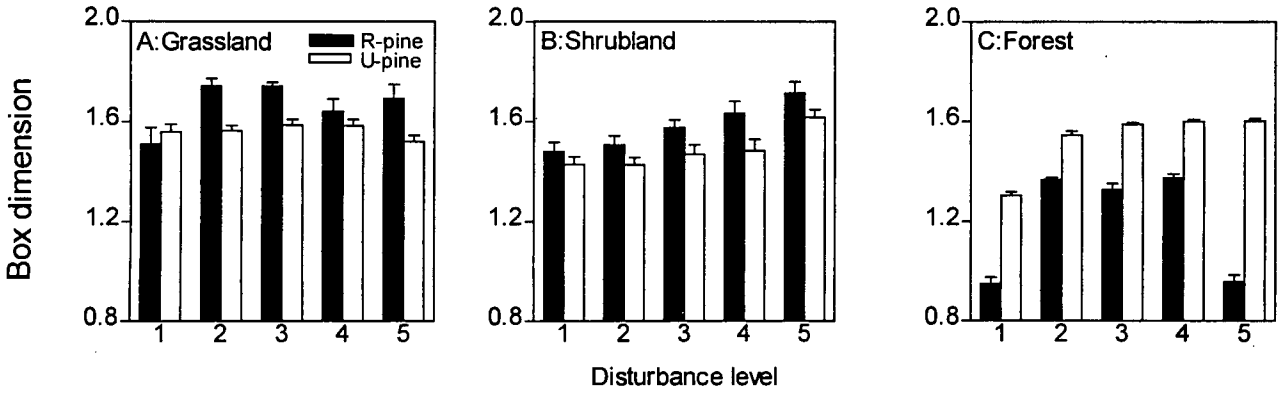

Figure 5. Mean and standard deviation (n=20) of the predicted box dimension for the R-pine and U-pine (*sensu* Keeley and Zedler 1998) under 5 levels of disturbance and in three environments (A=grassland, B=shrubland, C=forest).

Box dimension

The full factorial analysis of variance showed all factors and their interactions influenced the box dimension (Figure 4). As was the case for invasion rate the interactions accounted for much of the variation in the data; this implies that the main effects must be interpreted cautiously (Figure 4). The main effects suggested that higher levels of disturbance tended to increase the box dimension (Figures 4, 5); this implies that in undisturbed conditions the pattern of invasion is scattered.

The main effect of forest was associated with lower box dimensions than either the grassland or the shrubland (Figures 4, 5), no doubt due to the higher spatial dispersion of recruitment opportunities in forest. The R-pine tended to have a lower box dimension than the U-pine (Figures 4, 5) although not in forest. The box dimension increased strongly with disturbance level in forest (Figure 5C), due to the more uniform distribution of recruitment opportunities in felled forests. The box dimension responded weakly to disturbance in shrubland (Figure 5B) and showed only a small response to disturbance in grassland (Figure 5A). The R-pine's box dimension responded most strongly to intermediate levels of disturbance in forest (Figure 5C); the same trend is observed in the U-pine's box dimension response in grassland (Figure 5A). The box dimension of both pine types increased linearly with disturbance level in shrublands (Figure 5B). The trends observed show similarity with both the invasion rate trends (Pearson coefficient = 0.758), suggesting that the rates and patterns of plant spread are highly correlated. A similar result was found in Chapter 3.

DISCUSSION

The model developed here integrates the effects of environment type (natural disturbance), human-induced changes to the natural disturbance regime, and plant attributes into a single framework. It shows how knowledge of these factors can be used to understand and predict invasions. It follows that the results of this study can be useful heuristically, and as a predictive tool. I first discuss the model's heuristic value and then address its potential predictive value.

Understanding plant invasions

Many authors have concluded that an integration of information on environment type, disturbance and plant attributes is needed for understanding the ecology of plant invasions (Hobbs and Humphries 1995). Most attempts at such integration have been reviews of case

studies that culminate in conceptual models of invasion. These conceptual models are, however, often contradicted by the results of "anomalous" case studies (Lodge 1993a). I can think of three possible sources of the failure to account for the anomalies: (1) because different processes can produce the same pattern and because the mechanism of a factor's influence is often not defined it is unclear if the causal (i.e. correct) factor has been invoked (mechanism anomaly); (2) a factor's influence may be masked by its interaction with other factors (interaction anomaly); and (3) another factor may cause the anomaly (true anomaly). The advantages of this modelling approach are that: it reduces the potential for mechanistic anomalies; and it considers interactions and therefore avoids interaction anomalies. This means that only true anomalies will contradict the invasion model. I discuss these ideas in more detail by considering three popular themes in the literature on invasions: (1) disturbance as a facilitator of invasions; (2) the traits of an invader; and (3) the barriers to invasion.

Disturbance and invasions

Many reviews have concluded that plant invasions are enhanced by disturbance, but some case studies show the opposite. A good example of the most common conclusion (disturbance facilitates invasion) is the study of Hobbs and Mooney (1991). While Huenneke et al. (1990) showed that disturbance was not necessary for invasions to proceed, Strang (1974) showed that disturbances could inhibit invasions. Hobbs and Atkins (1988), in an experimental study, showed that the effect of disturbance was strongly dependent on environment type. This study showed that although the main effect of increasing disturbance is to enhance invasion rates, plant type and environment type were strong interacting factors. The effects of these interactions were often as large as the main effect. The effect of disturbance on invasions is thus an example of the mechanism and interaction anomalies: because disturbance both kills plants and provides recruitment opportunities, the sign of its effect can change with plant type and disturbance intensity. This implies that the debate on whether or not disturbance facilitates invasions is futile, since the effect of disturbance is context specific.

Traits of the invader

Lodge (1993a) reviewed studies that have sought to profile the traits of successful invaders. Although he found much evidence to support the view that typical "r-strategist" traits enhance invasion potential, there were too many exceptions for this "rule" to be useful (Lodge 1993a). Rejmanek and Richardson (1996) adopted a more rigorous approach in attempting to identify the

traits of invasive woody plants. Although they identified low seed mass, short juvenile periods and short intervals between large seed crops as traits of invasive woody species, seed type (fleshy or dry) and dispersal vector had to be invoked as an *ad hoc* explanation of exceptions. It therefore seems that no plant trait or suite of plant traits is a guarantee of invasive success (Lodge 1993a, Chapter 2). This study showed that the success of a pine tree as an invader was highly dependent on the environment type. This suggests that the traits of a successful invader must be defined in terms of the environment and disturbance regime (Chapter 3). While qualitative traits (e.g. resprouting ability) may be independent of environment type, quantitative traits are likely to be highly dependent on environment type. Increases in seed production, often attributed to predator release in the receiving environment (e.g. Honig et al. 1992), is an example of a quantitative trait that can have major impacts on invasive success (Tilman 1997). While we may be able to identify that seed production is influenced by either the biotic resistance of the receiving environment (Mack 1996), the genetic diversity of the founder population (Mooney et al. 1986, Rejmanek 1996b), or history (Mack 1995), the *a priori* prediction of seed production in receiving environments is likely to remain intractable.

Barriers to invasions

The observed resistance of different environments to invasion (e.g. Knops et al. 1995) is often considered a positive function of the resident biota's competitive ability (e.g. Crawley 1986, Diamond and Case 1986, Case 1991), species richness (e.g. Elton 1958, Pimm 1984, Case 1991, Tilman 1997), predator effectiveness (e.g. Mack 1996) or biomass (e.g. Peart 1989). Exceptions to these rules abound. For instance, a growing number of studies suggest that species richness and invasive resistance may be negatively related for plant invasions (Knops et al. 1995, Robinson et al. 1995, Planty-Tabacchi et al. 1996, but see Tilman 1997). This species richness - invadability anomaly is an example of the mechanism anomaly. Rejmanek (1996a) proposed that functional diversity rather than its correlate - species diversity, cause resistance to invasion. Of the many potential mechanisms of resistance to invasion, I chose to investigate the effect of the spatial and temporal distribution of disturbance (recruitment and mortality) on invadability. The results showed that pine trees tended to invade grassland faster than shrubland and shrubland faster than forest (subject to interactions with plant type and disturbance). This result is consistent with the "low-biomass - greater-invadability" hypothesis (Crawley 1987, Peart 1989, Richardson and Bond 1991). Since biomass was not modelled, the relationship between biomass and invadability may not be causal. Hence invadability may be a function of the recruitment opportunities and mortality risks an environment provides, where the

definition of these invasion opportunities and risks varies with plant type. This implies that opportunities for invasion must be defined from an organism's perspective (e.g. Cross 1981). This effectively requires that the identification and definition of a vacant niche: notoriously difficult to define *a priori* and tautological when defined *a posteriori* (Crawley 1986, Crawley et al. 1996).

In summary, this study shows that: (1) a few factors, if considered mechanistically and interactively, can improve our understanding of invasions; and (2) by embedding mechanisms and interactions into a theory of invasions we substantially reduce the number of factors needed in an invasion model and therefore the need to unnecessarily invoke *ad hoc* explanations. I believe that too much emphasis in invasion theory has been given to the main effects of poorly defined factors. I advocate that the mechanisms of and interactions between the factors plant type, environment type and disturbance should be considered before other factors are invoked.

Predicting invasions

Pine invasion case study

An understanding of the interactions involved in an invasion case study allows the prediction of the circumstances, i.e. the combination of factors, which facilitate or impede invasion (Hobbs and Humphries 1995). It follows that this model can generate useful management predictions. For example, limiting human treefelling levels can prevent pine invasions in afromontane forests. Similarly, moderating grazing levels and promoting frequent and intense fires can control the invasion of montane grasslands. Invasions of fynbos shrublands can be slowed, but not stopped, by maintaining infrequent and hence intense fires. Grassland and shrubland systems should thus be allowed to burn when high fuel biomass and dry weather conditions coincide. This suggestion is supported by the observed exclusion of woody plants from chaparral and sagebrush-steppe due to the invasion of flammable grass species (Zedler et al. 1983, Whiseant 1990, D' Antonio and Vitousek 1992).

The qualitative predictions made by the model agree with available data on the invasion of pines into forests, shrublands and grasslands of the southern hemisphere (Richardson and Higgins 1998). The records on these invasions allow us to count the number of invasions reported for grassland, shrublands and forest environments; and the number of times that human disturbance has been implicated in facilitating the invasions. These data suggest that forest is the least

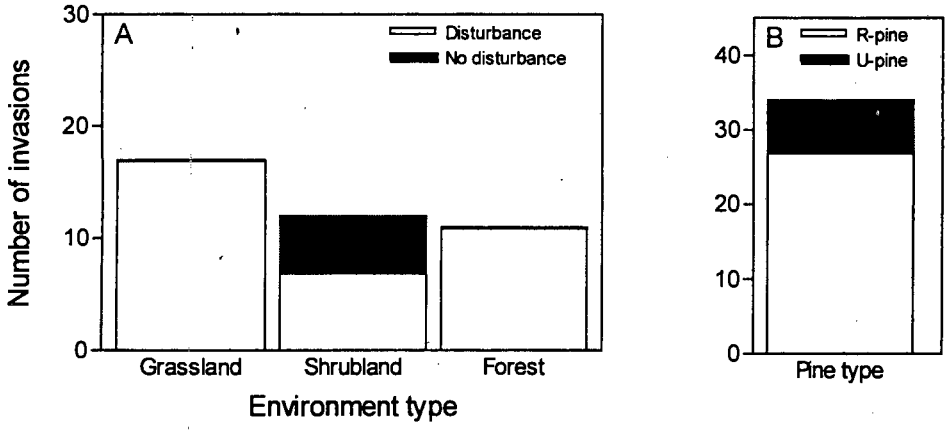

Figure 6. A: The number of invasions into grassland, shrubland, and forests of the southern hemisphere and whether disturbance was implicated in the invasion. B: The number of invasions by R- and U-pine types (*sensu* Keeley and Zedler 1998) in the southern hemisphere (after Richardson and Higgins 1998).

invadable environment type, and that grasslands and shrublands are more invadable (Figure 6A). The shrublands are the only environments where human disturbance is not always implicated in the invasion. Dividing these pine invasions into the R-pine and U-pine types (Figure 6B) shows that the R-pine is the more invasive type. This agrees with the model's predictions. However, the agreement between the model and these largely anecdotal records of pine invasions can only be considered as a weak form of validation. It is unfortunate that data for the more explicit testing of the model's predictions do not exist.

Applicability to other invasions

This study showed that generalisations are unlikely to emerge even within the confines of a model system. This means that details of these results will not be relevant for other plant types invading other types of environments subject to different recruitment opportunities and mortality risks. For instance, in some grasslands competition by vigorous grasses may reduce the recruitment probability of pine seedlings (Richardson and Bond 1991). What is transferable to other systems is an approach that concentrates on identifying invasion pathways, defining these pathways in functional terms, and integrating these terms into a spatially explicit simulation model. In this pine invasion example this resulted in a demographic model; other case studies may require a physiologically orientated approach (see Huston and Smith 1987). Hence, this approach is not a panacea for understanding and predicting invasions. The strength of the approach is that: (1) it can integrate the factors (correlates of these factors are often identified in comparative studies) that determine invasive success into a single model, and (2) the

mechanistic nature of the model allows the magnitude of the effects and interactive effects of these processes and phenomena to be estimated.

CONCLUSIONS

This study shows that the results of apparently contradictory case studies can be integrated into a general theory of plant invasions by explicitly considering the interactions between plant attributes, environment types, and disturbance levels. I believe that the model developed here has heuristic value. It demonstrates the need to shift perspective from the questions of "which plant attributes?" and "which environments?" (cf. SCOPE program: Drake et al. 1989) to questions of "which plant attributes in combination with which environments under which disturbance levels?" and "how do we define these plant attributes, environments and disturbance levels in a mechanistic framework?" This suggests that: factorial invasion experiments are needed (time consuming and expensive); invasion models must be more complex (data- and computationally demanding); and the comparative method will have to be applied with somewhat greater ingenuity (creatively taxing). It is also clear that model development, experimental design and data collection should be more closely integrated than is the case at present.

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Appendix 1. Model factors used in the factorial experimental design and the model settings for each factor combination in modelling the invasion of two pine types in three environments under 5 levels of disturbance.

Factors					Model functions and constants					
D[1]	E[2]	P[3]	Disturb. type	Fall quota	Ignition probability	Spread threshold	Mortality probability	Shade toler.	Recruitment capacity	Type seed release
1	G	R	Fire	-	$1/(1+10^{2\text{-veg.age}})$	1±0.5	$1[0.5+0.45/(1+10^{0.4(age-10)})]$	0	$40/(1+10^{0.4(7-age)})$	Serotinous
2	G	R	fire	-	$1/(1+10^{2\text{-veg.age}})$	2±1	$0.8[0.5+0.45/(1+10^{0.4(age-10)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
3	G	R	fire	-	$1/(1+10^{2\text{-veg.age}})$	4±2	$0.6[0.5+0.45/(1+10^{0.4(age-10)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
4	G	R	fire	-	$1/(1+10^{2\text{-veg.age}})$	6±3	$0.4[0.5+0.45/(1+10^{0.4(age-10)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
5	G	R	fire	-	$1/(1+10^{20\text{-veg.age}})$	8±4	$0.2[0.5+0.45/(1+10^{0.4(age-10)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
1	S	R	fire	-	$1/(1+10^{16\text{-veg.age}})$	4±2	$1[0.7+0.25/(1+10^{0.4(age-14)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
2	S	R	fire	-	$1/(1+10^{12\text{-veg.age}})$	4±2	$0.8[0.7+0.25/(1+10^{0.4(age-14)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
3	S	R	fire	-	$1/(1+10^{8\text{-veg.age}})$	4±2	$0.6[0.7+0.25/(1+10^{0.4(age-14)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
4	S	R	fire	-	$1/(1+10^{4\text{-veg.age}})$	4±2	$0.4[0.7+0.25/(1+10^{0.4(age-14)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
5	S	R	fire	-	$1/(1+10^{2\text{-veg.age}})$	4±2	$0.2[0.7+0.25/(1+10^{0.4(age-14)})]$	0	$40/(1+10^{0.4(7-age)})$	serotinous
1	F	R	fall	1%	-	-	1	0	$40/(1+10^{0.4(7-age)})$	serotinous
2	F	R	fall	2%	-	-	1	0	$40/(1+10^{0.4(7-age)})$	serotinous
3	F	R	fall	4%	-	-	1	0	$40/(1+10^{0.4(7-age)})$	serotinous
4	F	R	fall	8%	-	-	1	0	$40/(1+10^{0.4(7-age)})$	serotinous
5	F	R	fall	16%	-	-	1	0	$40/(1+10^{0.4(7-age)})$	serotinous
1	G	U	fire	-	$1/(1+10^{2\text{-veg.age}})$	1±0.5	$1[0.2+0.75/(1+10^{0.4(age-8)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
2	G	U	fire	-	$1/(1+10^{2\text{-veg.age}})$	2±1	$0.8[0.2+0.75/(1+10^{0.4(age-8)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
3	G	U	fire	-	$1/(1+10^{2\text{-veg.age}})$	4±2	$0.6[0.2+0.75/(1+10^{0.4(age-8)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
4	G	U	fire	-	$1/(1+10^{2\text{-veg.age}})$	6±3	$0.4[0.2+0.75/(1+10^{0.4(age-8)})]$	1	$40/(1+10^{0.4(7-age)})$	mast
5	G	U	fire	-	$1/(1+10^{2\text{-veg.age}})$	8±4	$0.2[0.2+0.75/(1+10^{0.4(age-8)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
1	S	U	fire	-	$1/(1+10^{20\text{-veg.age}})$	4±2	$1[0.4+0.75/(1+10^{0.4(age-12)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
2	S	U	fire	-	$1/(1+10^{16\text{-veg.age}})$	4±2	$0.8[0.4+0.75/(1+10^{0.4(age-12)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
3	S	U	fire	-	$1/(1+10^{12\text{-veg.age}})$	4±2	$0.6[0.4+0.75/(1+10^{0.4(age-12)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
4	S	U	fire	-	$1/(1+10^{8\text{-veg.age}})$	4±2	$0.4[0.4+0.75/(1+10^{0.4(age-12)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
5	S	U	fire	-	$1/(1+10^{4\text{-veg.age}})$	4±2	$0.2[0.4+0.75/(1+10^{0.4(age-12)})]$	1	$40/(1+10^{0.4(13-age)})$	mast
1	F	U	fall	1%	-	-	1	1	$40/(1+10^{0.4(13-age)})$	mast
2	F	U	fall	2%	-	-	1	1	$40/(1+10^{0.4(13-age)})$	mast
3	F	U	fall	4%	-	-	1	1	$40/(1+10^{0.4(13-age)})$	mast
4	F	U	fall	8%	-	-	1	1	$40/(1+10^{0.4(13-age)})$	mast
5	F	U	fall	16%	-	-	1	1	$40/(1+10^{0.4(13-age)})$	mast

1: D=disturbance; numbers refer to disturbance levels. 2: E=environment type; G=grassland, S=shrubland, F= forest. 3:=pine type; R=R-pine, U=U-pine.

CHAPTER 5

PREDICTING PLANT MIGRATION RATES IN A CHANGING WORLD: THE ROLE OF LONG-DISTANCE DISPERSAL

Abstract. Models of plant migration based on estimates of biological parameters severely underestimate the rate of spread when compared to empirical estimates of plant migration rates. This is disturbing, since an ability to predict migration and colonisation rates is needed for predicting how native species will distribute themselves in response to habitat fragmentation and climate change and how rapidly invasive species will spread. Part of the problem is the difficulty of formally including rare long-distance dispersal events in spread models. In this chapter I explore the process of making predictions about plant migration rates. In particular I examine the links between data, statistical models and ecological predictions. I fit mixtures of Weibull distributions to several dispersal data sets and show that statistical and biological criterion for selecting the most appropriate statistical model conflict. Fitting a two-component mixture model to the same data increases the spread rate prediction by an average factor of 4.5. Data limits our ability to fit more components. Using simulations I show that a small proportion (0.001) of seeds moving long-distances (1-10 km) can lead to an order of magnitude increase in predicted spread rate. The analysis also suggests that most existing data sets on dispersal will not resolve the problem. Dispersal had the strongest effect on the predicted spread rate. Fragmentation level and fecundity also strongly influenced the predicted spread rate whereas age of reproductive maturity and fire return interval were less important. I predict that when long-distance dispersal occurs that plant migration rates will decrease linearly with increasing levels of fragmentation. This prediction is in contrast to the sharply non-linear thresholds predicted by percolation theory.

Key words: Mixture models, *Pinus*, biological invasions, global change, fragmentation, percolation theory, landscape connectivity.

INTRODUCTION

Ecologists face the challenge of predicting how organisms will respond to global change. Plants could respond by changing their physiology, phenology, or resource allocation patterns. In addition, plants may shift their ranges as environmental conditions change. Two issues complicate our ability to predict the rates of these range shifts. First, causal links between

climatic parameters and plant behaviour are difficult to establish (Woodward 1992). Second, addressing whether plants will be able to reach sites where environmental conditions are suitable needs a better understanding of migration processes (Pitelka 1997).

The movement of a plant population across a landscape is a function of population growth, dispersal, the availability of suitable recruitment opportunities and landscape structure. Previous work has concentrated on the effect of population growth (e.g. Chapter 3), the distribution of recruitment opportunities (e.g. Chapter 4), and fragmentation patterns (e.g. Malanson and Cairns 1997) on migration rates. Despite the recognised importance of dispersal in the dynamics of populations (Harper 1977), modelling of dispersal has been limited by the statistical methods available for describing dispersal (Beuchner 1987, Okubo and Levin 1989, Willson 1993, Portnoy and Willson 1993). This inadequate treatment of dispersal means that we cannot tell whether migration rates are limited by the availability of suitable climates, recruitment opportunities, life history attributes, landscape structure or by dispersal (Woods and Davis 1989). The primary aim of this paper is to explore the neglected process of defining and parameterising the dispersal components of a plant spread model.

Previous models of plant spread have tended to use dispersal functions that are not explicitly linked to data. The criteria used for "parameterising" these dispersal functions vary, but typically the parameterisation is directed at getting the model to exhibit "realistic behaviour" (Schwartz 1992, Dyer 1995, Collingham et al. 1996, Ibrahim et al. 1996, Malanson and Armstrong 1996, Le Corre et al. 1997, Malanson and Cairns 1997). Approaches that have been linked to data have used short-tailed dispersal functions. Short-tailed dispersal functions include the normal, log-normal, inverse power law, Weibull and exponential distributions. Short-tailed distributions can be parameterised from empirical data sets using standard statistical techniques (e.g. Okubo and Levin 1989, Willson 1993). Unfortunately because short-tailed dispersal functions concentrate on local dispersal, a spread model that uses a short-tailed distribution does not yield "realistic behaviour". For instance Skellam (1951) could not get his reaction-diffusion model to predict post-glacial oak migration rates and he invoked rare long-distance dispersal events to explain the rapid migration. Similarly Reynolds (1954) concluded that dispersal by Kangaroo rats could not explain the rapid invasion of mesquite into rangelands in Arizona, and invoked long-distance dispersal by cattle. More recently it has been shown that biologically unreasonable parameterisations of reaction-diffusion models are needed to get them to match observed migration for a range of tree (Birks 1989) and herbaceous species (Cain et al. 1998). Ecological spread models that ignore long- distance dispersal tend to predict spread rates of 1 -

50 meters per year (Skellam 1951, Chapter 3). The rapid migration of trees after the last post-glacial (50 -1000 m/yr; Delcourt and Delcourt 1987, Birks 1989) and the rate of some contemporary invasions (5-13 km/yr; Plummer and Keever 1963, Mack 1981) suggests that rare long-distance dispersal is a widespread phenomenon that cannot be ignored.

This discrepancy between observed spread rates and model predictions implies that existing protocols for making spread rate predictions are inadequate. I hypothesise that the links between data, the statistical description of these data, and spread models can explain these discrepancies. The essence of the problem lies in the failure of existing approaches to incorporate rare long-distance dispersal events. In other words there has been an inability to formalise in spread models the stratified nature of invasion and migration processes (Pielou 1979, Moody and Mack 1988, Hengeveld 1989, Wilson and Lee 1989). Until recently the description of rare long-distance dispersal events, caused by the unusual behaviour of dispersal vectors, was relegated to the anecdotal end of the dispersal literature (van der Pijl 1983, Davis 1987, Wilkinson 1997). Recent contributions (Shigesada et al. 1995, Kot et al. 1996, Clark 1998) have made valuable progress towards describing and modelling stratified diffusion processes. Shigesada et al. (1995) modified Skellam's reaction diffusion model to include rare long-distance dispersal. Kot et al. (1996) fitted a variety of fat-tailed distributions to *Drosophila pseudoobscura* dispersal data. Similarly, Clark (1998) refined Ribbens et al.'s (1994) method for parameterising dispersal distributions from maps of adult trees and seeds by fitting fat-tailed dispersal distributions. Both Kot et al. (1996) and Clark (1988) used integro-difference equations to make spread rate predictions. These approaches were all capable of predicting rapid migration using empirically based dispersal functions. I explore a third approach that fits mixture models to frequency distributions of dispersal data and integrates these statistical models with an individual-based spatial simulation model. Mixture models are designed to describe samples from heterogeneous populations; this makes them particularly suited to describing dispersal data sets since these data are often the product of several underlying dispersal processes. In fact most of the examples of migration models that use data-free dispersal functions (cited above) conceptually used a mixture of dispersal functions. While multi-vector dispersal systems immediately come to mind as a mixture distribution, even single-vector dispersal systems are likely to be the product of a variety of dispersal processes. For instance, the gyroscopic seeds of some pine species can be divided into three populations. The first population consists of seeds that are released at wind velocities too low for the seeds to rotate, or at the wrong angle for rotation: these seeds fall close to the parent canopy. The second population consists of seeds released in winds of sufficient strength for the seed to rotate, but

not generate lift: these seeds fly moderate distances. The third population consists of seeds released in winds strong enough to generate lift from the spinning samara: these seeds can travel considerable distances.

Despite its importance, dispersal is but one factor among the interacting factors which influence plant migration; other factors are climate suitability, resource availability, disturbance, fragmentation, fecundity, mortality, generation time and age of reproductive maturity. Any attempt to explore the effects of how dispersal is modelled must take account of all these factors and the interactions between them. For this reason I use a spatially explicit, individual-based simulation model that simulates the interactions between life-history attributes, disturbance and environment (Chapters 3 and 4) as the basis for this study. This model allows us to explore the details of the spatial demographic process of plant migration through landscapes. Percolation theory has emerged as the dominant paradigm that defines the movement of organisms through landscapes. Percolation theory makes two important predictions. First it predicts that landscapes with at least a proportion of 0.5928 of suitable habitat will allow an organism to percolate through the landscape (Gardner et al. 1987). Applications of percolation theory, however, recognise that the proportion of habitat needed for percolation will vary from 0.5928 depending on the arrangement of suitable habitat in the landscape and whether the organism perceives the landscape as connected (With and Crist 1995, Wiens et al. 1997, With et al. 1997). The second prediction of percolation theory is that organisms will respond in a non-linear way to decreasing connectivity of the landscape; i.e. small changes in landscape connectivity near some critical threshold are predicted to have large effects on the organisms migration potential (With 1997). Although most percolation papers use the term organism, most authors clearly have animals in mind and tests of percolation theory have been limited to animal applications (e.g. With and Crist 1995, Wiens et al. 1997). I was interested in exploring whether percolation theory is a useful construct for thinking about plant movement in fragmented landscapes. A question of more general relevance to the understanding of the migration of organisms is whether the predictions of percolation theory break down when rare long-distance dispersal events occur.

The aim of this paper is to develop the links between dispersal data, the statistical description of data, and the predictions of plant migration models. In particular I ask: (1) Are existing data sets, and hence methods of data collection adequate? (2) Can alternative statistical approaches improve our statistical description of rare long-distance dispersal events? (3) Does data or statistical methodology limit our ability to predict spread rates? (4) Do plant migration rates

respond in a non-linear way to increasing fragmentation levels, and how is this influenced by long-distance dispersal? (5) How does the form of the dispersal function interact with plant life-history attributes, disturbance regime, and fragmentation pattern in influencing the predicted spread rate? I explore these questions by using pine tree invasions into fire-prone shrublands of South Africa as a case study.

METHODS

Data sources

I collected data on *Pinus pinaster* dispersal and used Greene and Johnson's (1989) data on *P. contorta* dispersal. I collected data in a similar way to Greene and Johnson: *P. pinaster* seeds were released from a height of 2 m on an open field under moderate wind conditions (0.5-3 m/s) and the distance travelled by each seed was recorded. The objective was to characterise a frequency distribution of distances travelled by seeds. Approximately 200 seeds were released on three separate occasions, yielding three data sets.

Statistical methods

I used MIX 2.3 (Macdonald and Green 1988) to fit one-, two- and three-component mixtures of Weibull and exponential distributions. MIX uses maximum-likelihood estimation for grouped data to fit the distributions. The mixed probability density function g is a weighted sum of k component densities,

$$g(x) = p_1 b_1 c_1 (b_1 x)^{c_1 - 1} \exp\left\{-(b_1 x)^{c_1}\right\} + \ldots + p_k b_k c_k (b_k x)^{c_k - 1} \exp\left\{-(b_k x)^{c_k}\right\} \quad (1)$$

The parameters are the mixing proportions (p_n) the scale (b_n) and shape (c_n) parameters of the nth component Weibull distribution (the exponential is a special case of the Weibull when c=1). The notation for parameter vectors for a mixture of three Weibull distributions that I will use in this paper is (p_1, p_2, p_3; b_1, b_2, b_3; c_1, c_2, c_3). The procedure I followed was to fit a one-component Weibull distribution to the data, and then a mixture of two Weibull distributions (a two-component model) and then three-component model. Log-likelihood ratios were used to evaluate the fit of the different models.

Preliminary attempts to fit three-component mixture models suggested that the sample sizes of the available data were too small. This meant that a third, long-distance dispersal, component

could not be fitted. I approached this problem in two ways. First I asked whether the fit of the two-component model would changed if a third (long-distance dispersal) component was added. This was done by exploring the changes in the log-likelihood ratio for a range of parameterisations ($0.001 < p_3 < 0.01$; $0.0001 < b_3 < 0.001$; $c_3 = 1$) of the third component. This allows the assessment of whether the fit of the model is substantially improved or worsened by the inclusion of the third long-distance dispersal component. Second, I used simulated data sets to estimate the sample size needed to estimate a dispersal distribution that included a long-distance dispersal component. This involved generating random data sets of known parameter values and investigating the sample size needed by the maximum-likelihood method to recover these parameters.

Spread rate predictions

The model developed in Chapters 3 and 4 was used to make spread rate predictions. The model was developed to simulate the spread of alien pine trees in the Mediterranean shrublands (fynbos) of South Africa. This model, a spatially explicit, individual-based simulation (SEIBS) model simulates the growth, mortality, dispersal and recruitment of pine trees in a fire-dominated environment. Pine trees invading fynbos are subject to high levels of fire-induced mortality, but their serotinous habit and fecundity means that they compete well for recruitment opportunities in the post-fire environment (Richardson and Higgins 1998). In this application I use typical parameter estimates for *Pinus pinaster* (Chapters 3 and 4) invading fynbos. A fecundity level of 5 recruits per adult tree of 10 cm dbh (see Ribbens et al. 1994, Chapter 6), an age of reproductive maturity of 6 years, and a 10 year fire return interval were used for the baseline simulations. Since the model is not sensitive to the range of fire-induced mortality levels observed in fynbos (Chapter 3), this was held constant throughout. The dispersal function of the original SEIBS model was modified from an exponential function to a three-component mixture of Weibull distributions. The different statistical parameterisations of the mixture dispersal function (discussed above) were then used to explore the impacts on spread rate.

To explore the effects of fragmentation, the model was run under conditions of 0.1,0.2,0.3,...,0.9 of the landscape fragmented. I used the same method as With et al. (1997) to generate fragmented landscapes, but I only considered two landscape types (suitable and unsuitable). The midpoint displacement algorithm (Saupe 1988) was used to produce fractal landscapes. The midpoint displacement algorithm has two parameters H (spatial dependence of points) and σ^2 (variance in displacement of points). Moving H from 0 to 1 increases the level of

aggregation. Following With et al. (1997) I set H to 0.5 and σ^2 to 1. The fractal dimension of the landscapes generated by the algorithm is equal to 3.0-H, i.e. 2.5 for this study. The midpoint algorithm produces a three dimensional surface and I was interested in classifying the landscape into suitable and unsuitable habitat; to do this I sequentially defined the highest points in the landscape as unsuitable habitat until the required amount of unsuitable habitat was met.

The importance of long-distance dispersal in influencing migration rates is likely to be influenced by interactions with life-history attributes, disturbance regime and fragmentation pattern. A separate sensitivity analysis that summarised and integrated the effects of these factors was run. A 2^5 factorial experimental design quantified the interactive effects dispersal, fecundity, age of reproductive maturity, fire return interval and fragmentation (Table 1).

Table 1. Factor levels used in the 2^5 factorial sensitivity analysis. Dispersal is the dispersal vector; Fecundity is the number of recruits produced by a tree of 10 cm dbh.

Factor	Level 1	Level 2
Dispersal	(0.9,0.05,0.0; 0.2,0.02,0.0; 1,1,0.0)	(0.9,0.099,0.001; 0.2,0.02,0.0002; 1,1,1)
Fecundity	2	15
Age of reproduction	20	6
Fire return interval	25	8
Fragmentation	0.7	0

The most distant plant from the source population was used to record the distance travelled by the population. This was regressed against time to estimate the spread rate. Each simulation was initiated with a population of 1000 plants arranged as a plantation on the edge of a rectangular grid of 100x4 000 cells. Each cell was assumed to represent a 10x10 m area. Smaller landscapes (100x512 cells) were used for the runs that included fragmentation as a factor. All simulations were run for 50 years, this was long enough to get an unbiased estimate of the spread rate.

RESULTS

Statistical models

Preliminary model fitting showed that when a one-component model was fitted to the data a Weibull distribution fitted the data best. When a two-component model was fitted, the maximum-likelihood method converged on a shape parameter that made the distribution right-skewed ($c > 3.602$). This does not make biological sense, as most seed shodows are left

Table 2. Parameter estimates for fitted mixture models of *Pinus contorta* and *P. pinaster* seed distribution data. G is the log-likelihood statistic (* indicates $p < 0.05$) and AIC is the Akaike Information Criterion. *s* is the number of fitted parameters.

	Component 1			Component 2					
Data set	p_1	b_1	c_1	p_2	b_2	c_2	G	s	AIC
contorta1	1.000	0.1460	1.699				9.901*	2	13.90
contorta1	0.958	0.1532	1.834	0.042	0.0436	1.000	6.140*	4	14.14
contorta2	1.000	0.0699	1.759				19.85*	2	23.85
contorta2	0.951	0.0750	1.953	0.049	0.0094	1.000	13.31*	4	21.31
contorta3	1.000	0.1943	1.470				15.26*	2	19.26
contorta3	0.971	0.2034	1.564	0.029	0.0430	1.000	11.97*	4	19.97
contorta4	1.000	0.0505	1.814				19.61*	2	23.61
contorta4	0.961	0.0534	1.972	0.039	0.0084	1.000	15.57*	4	23.57
pinaster1	1.000	0.1251	1.134				64.82	2	68.82
pinaster1	0.928	0.1495	1.668	0.072	0.0211	1.000	8.819*	4	16.82
pinaster2	1.000	0.0758	1.006				123.8	2	127.8
pinaster2	0.814	0.0115	2.158	0.186	0.0247	1.000	16.17*	4	24.17
pinaster3	1.000	0.1143	1.000				162.4	1	164.4
pinaster3	0.899	0.4044	1.000	0.101	0.0158	1.000	1.382*	3	7.382

kewed (Okubo and Levin 1989), and I consequently constrained the second and third components to be exponential distributions ($c = 1$).

The fits of the empirical data (Table 2) show that the two-component mixture models fitted the data better than one-component mixture models. The model with the lowest AIC (Akaike's Information Criterion) is statistically the best model. The log-likelihood ratio was examined to see if adding a third component would change the fit of model. Lower log-likelihood values suggested that this third component often improved the fit of the model (decreased the log-likelihood, Figure 1) and never substantially worsened the fit (increased the log-likelihood). The contour plots (Figure 1) also show that the fit of the model is more sensitive to p_3 (the proportion of seeds in the third component) than to b_3 (the scale parameter of the third component). However, using the principle of a likelihood ratio test, it is clear that the fit of the three-component model is never significantly better than the two-component model. For the three-component model to be better than the two-component model the log-likelihood must change by 5.991 (χ^2 critical value for two degrees of freedom). This suggests that since adding a third component does not significantly improve the fit we should, on statistical grounds, select the two-component models.

I generated simulated data sets of sample sizes 200 (about the size of the empirical data sets used here), 10^3, 10^4 and 10^5 observations. All data sets had a vector of (0.9,0.099,0.001; 0.1,0.01,0.0001; 1,1,1). The resulting fits to these data are shown in Table 3. For all data sets the first two-components of the mixture model were well estimated. For the data set of

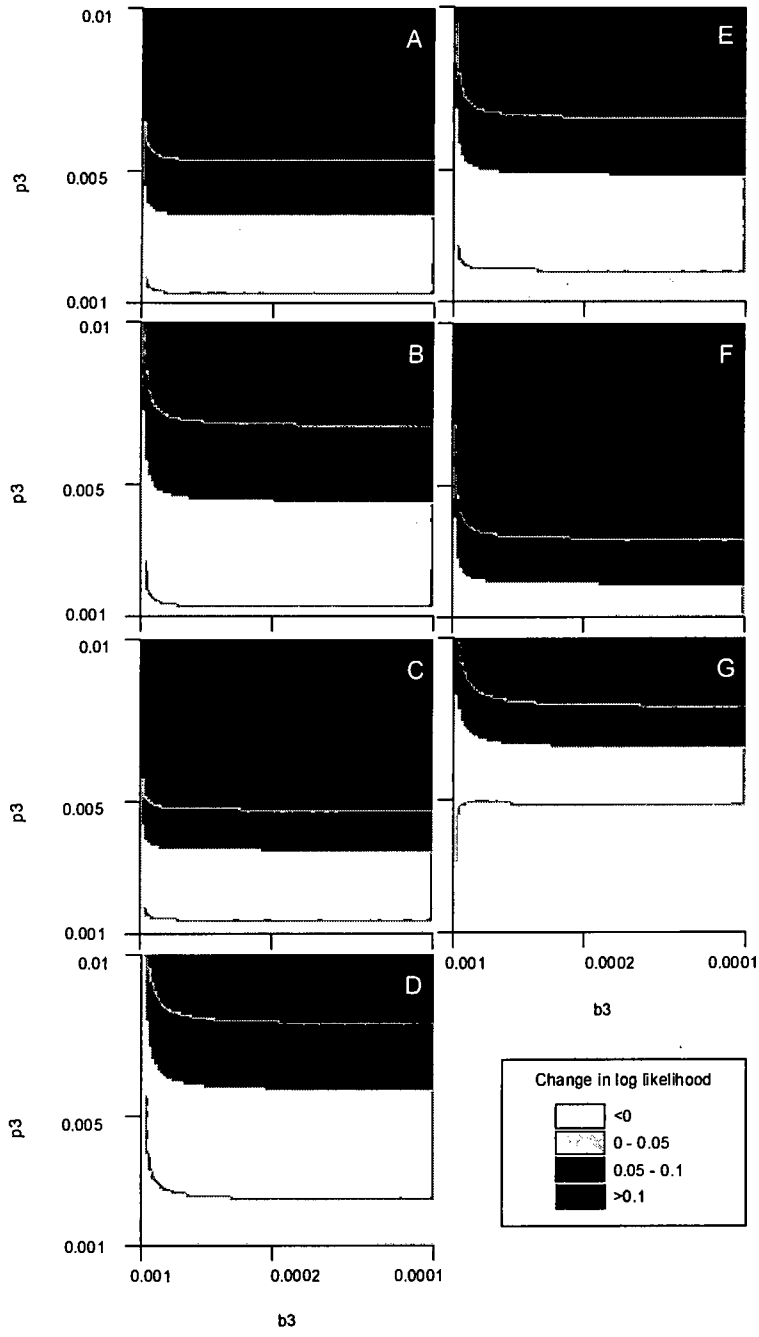

Figure 1. Changes in log-likelihood of a two-component mixture model of seven dispersal data sets (Table 2) with the inclusion of a third component that describes rare long-distance dispersal. p_3 is the proportion of seeds dispersed by this third component and b_3 is the scale parameter of this third component. Reductions in the log-likelihood indicate an improved fit, increases in the log-likelihood indicate a worse fit.

Table 3. Parameter estimates for fitted mixture models of simulated dispersal data sets of different sizes. G is the log-likelihood statistic (* indicates $p<0.05$), *s* is the number of fitted parameters.

Sample	Component 1			Component 2			Component 3				
Size	p_1	b_1	c_1	p_2	b_2	c_2	p_3	b_3	c_3	G	s
200	0.907	0.106	1.000	0.093	0.0091	1.000	-	-	-	15.847*	3
10^3	0.886	0.105	1.000	0.112	0.010	1.000	0.001	0.0005	1.000	30.547*	5
10^4	0.895	0.105	1.000	0.104	0.010	1.000	0.001	0.0001	1.000	25.496*	5
10^5	0.896	0.106	1.000	0.103	0.010	1.000	0.001	0.0001	1.000	22.708*	5

200 observations b_3 could not be estimated; only a two-component model could be fitted. The 1000 observation data sample was large enough for a third component distribution to be fitted; however, the magnitude of this third component was underestimated (Table 3). The 10^4 and 10^5 observation data sets yielded adequate parameter estimates (Table 3). This analysis suggests that sample-sizes in the order of 10^4 are needed for fitting a long-distance dispersal model.

Spread rates

Most of the one-component models predict spread rates below 6 m/yr (mean = 1.78 m/yr, Figure 2); whereas the two-component models predict spread rates between 1 and 26 m/yr (mean = 8.11 m/yr, Figure 2). This means that fitting a two-component mixture model to the same data increases the spread rate prediction by an average factor of 4.5. The spread rates predicted by models parameterised with simulated seed dispersal data sets (Table 3, Figure 3) show how larger data sets would translate into spread rates differing by an order of magnitude.

The spread rate predictions for simulations run over a range of possible parameterisations (see Figure 1) of three-component models are shown in Figure 4A. Increasing p_3 and decreasing b_3 increases the migration rate. The migration rate seems equally sensitive to these two parameters in contrast to the fit of the mixture model, which was more sensitive to p_3 (Figure 1). These simulations show how a small proportion (0.001) of seeds moving long-distances (1-10 km) can lead to an order of magnitude increase in predicted spread rate (compare Figure 2 with Figure 4A). The variation in the predicted spread rate between simulations is high (Figure 4B); this illustrates that it is the rare long-distance dispersal events that strongly influence the predicted spread rate

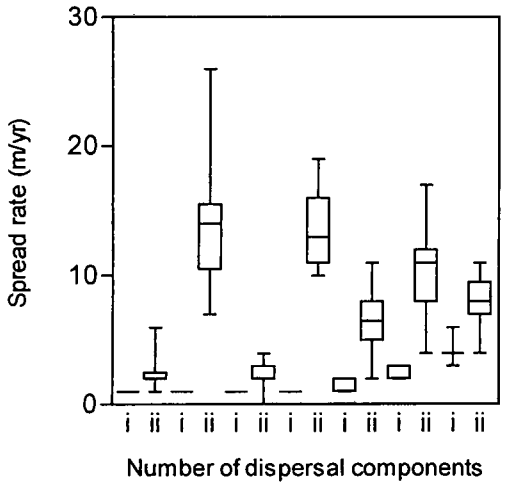

Figure 2. Spread rate predictions of the SEIBS model using one- and two-component mixture models to describe dispersal. Data from seven data sets (Table 2) were used to fit the mixture models.

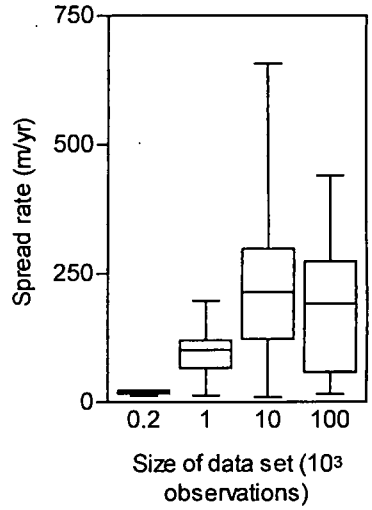

Figure 3. Spread rate predictions of the SEIBS model using mixture models fitted to simulated data sets of increasing size (Table 3).

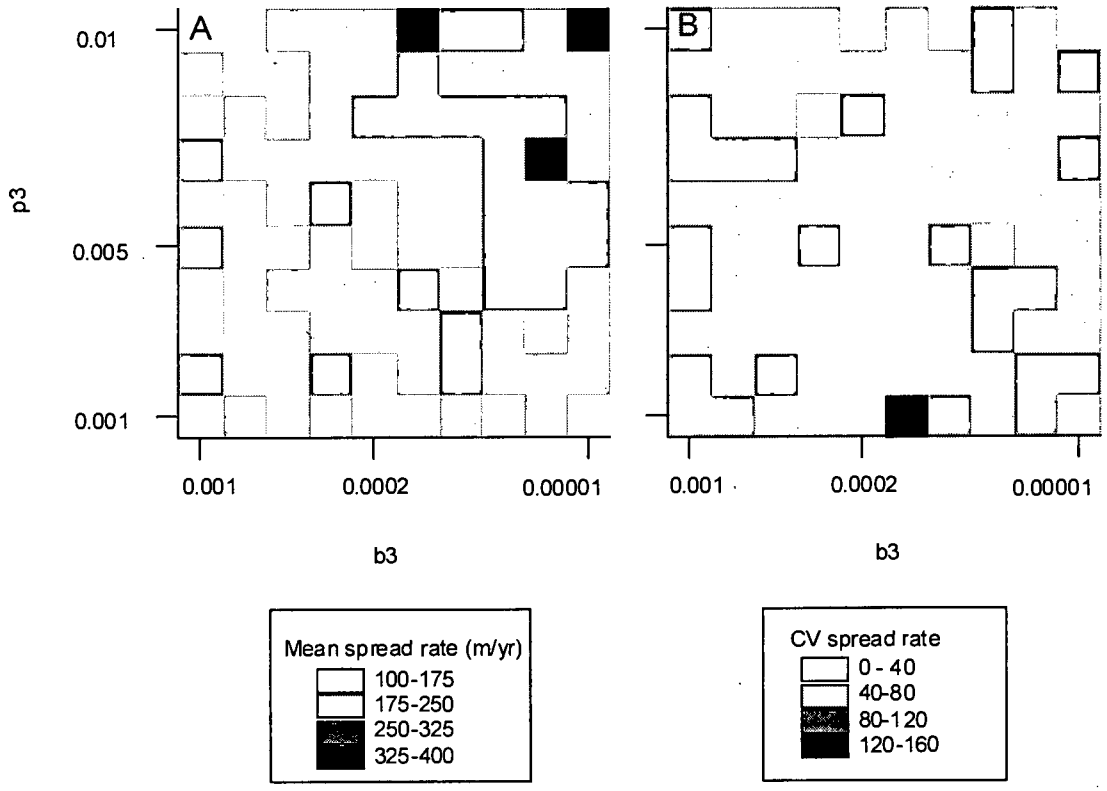

Figure 4. The mean (A) and CV (B) of the predicted spread rates for different parameterisations of the third component of a mixture model (see Figure 1 for the statistical fits of these parameterisations). Spread rates were predicted using the SEIBS model.

Fragmentation effects

The mean of the predicted spread rate decreased with increasing level of fragmentation for both the local dispersal model and for the long-distance dispersal model (Figures 5A and 5C). The reason that the poorly-dispersed populations were little affected by increasing levels of fragmentation was that they spread slowly and were consequently only rarely confronted by a fragment border. In highly fragmented landscapes they confronted the fragment border sooner. This explains the linear response (not significantly non-linear; runs test, $p=0.345$) of the local dispersal model to increasing fragmentation (Figure 5A). The model that included long-distance dispersal was also not significantly non-linear (runs test, $p=0.643$). Migration rates were not influenced by low levels of fragmentation but decreased linearly between 0.5 and 0.9 of the landscape fragmented (Figure 5C).

The largest single dispersal event was also recorded for each simulation run (Figures 5B and 5D). This is a more effective method of detecting the thresholds of landscape connectivity. Hence for the model that included only local dispersal, a threshold of landscape connectivity may exist when fragments are more than 400-500 m apart (Figure 5B). Under this assumption of long-distance dispersal this threshold could exist in landscapes with nearest-fragment distances of between 3000-5000 m (Figure 5D).

Interactions between dispersal, life history, disturbance and fragmentation

The interactions between dispersal, fecundity, age of reproductive maturity, fire-return interval and fragmentation were investigated using a factorial experimental design (Figure 6). This analysis showed that, for the range of parameterisations explored, dispersal has the strongest effect on the predicted spread rate. Fragmentation level and fecundity also strongly influenced the predicted spread rate. Age of reproductive maturity and fire return interval were of lesser importance. Many of the interactions were large in magnitude. These interactions can be interpreted as follows. The interaction between dispersal and fecundity occurs since the more seeds a plant produces, the more long-distance colonists it will produce. The need for colonists to land in suitable habitat explains the interactions between dispersal and fragmentation, between dispersal and fire frequency, between fire frequency and fragmentation, and the third-order interaction between dispersal, fire-frequency and fragmentation. The negative interaction between age of reproductive maturity and fire frequency occurs because slow-maturing plants growing in landscapes subject to frequent fires will not be able to replace themselves after

suffering fire mortality. Moreover, they will be unable to take advantage of the recruitment opportunities offered by the post fire-environment.

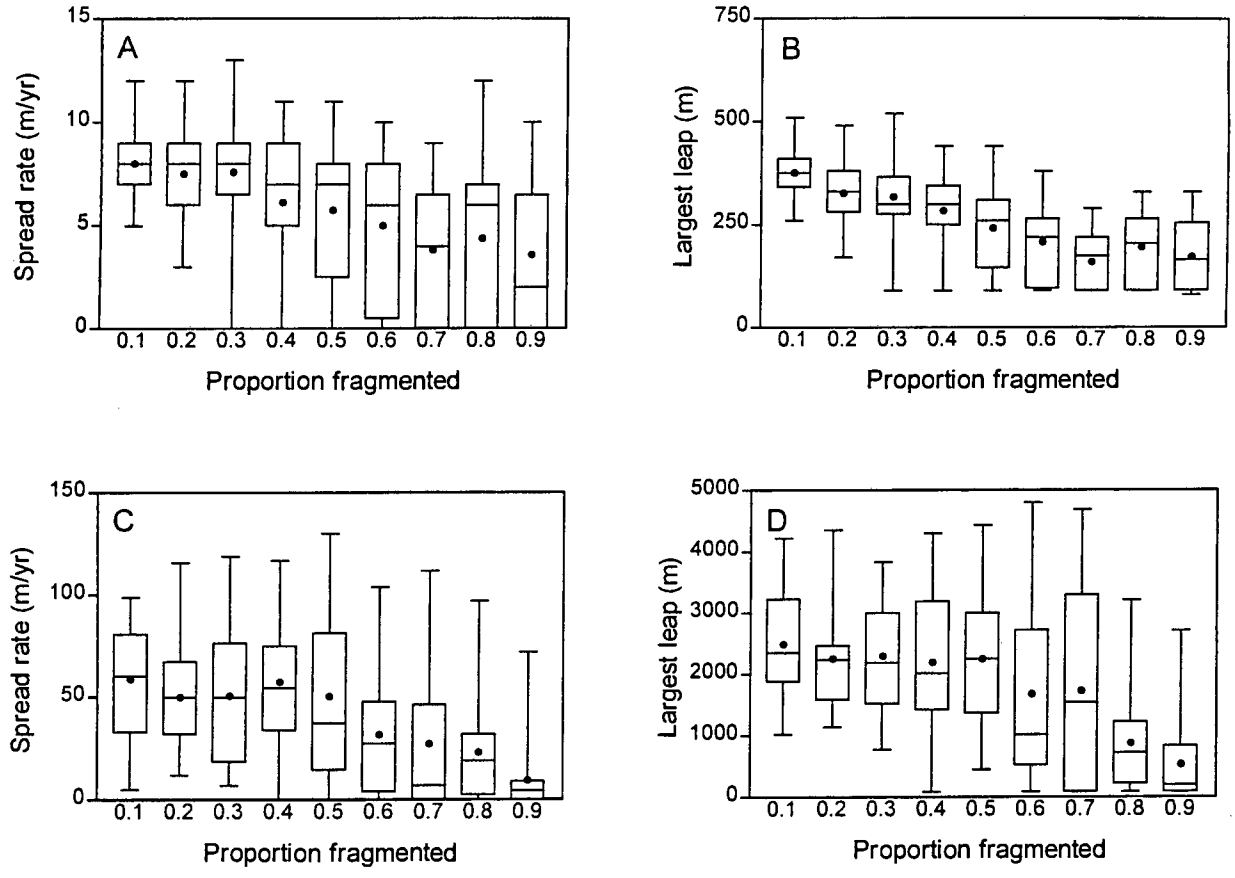

Figure 5. The spread rate and largest leap (largest single dispersal event in a simulation run) predictions as a function of fragmentation level for models that simulate short distance dispersal (A and B) and both long and short distance dispersal (C and D). Predictions were made using the SEIBS model.

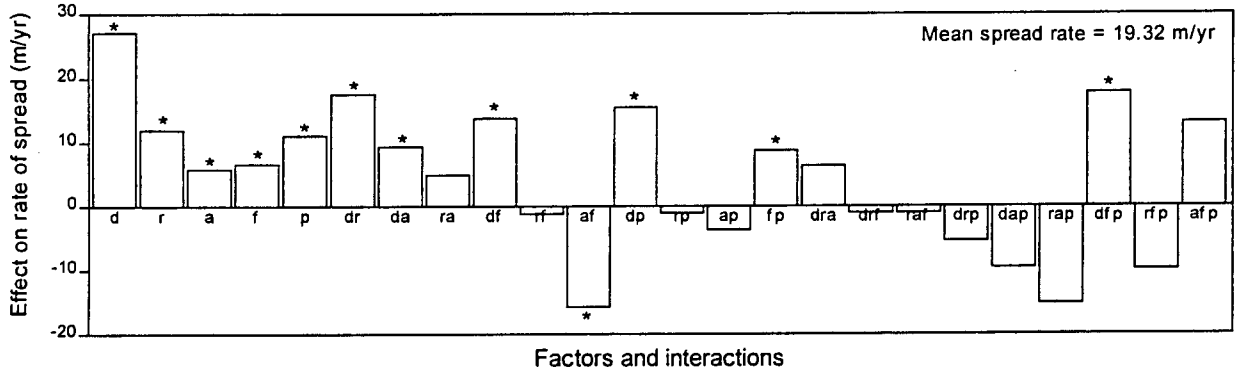

Figure 6. The effect of dispersal function (d), fecundity (r), age of reproduction (a), fire-return interval (f) and fragmentation (p) and their interactions on the predicted rate of spread. Effects were estimated using a 2^5 factorial design of SEIBS simulation runs (Table 1). * Indicates significant effects ($p<0.05$).

DISCUSSION

I have shown that a consideration of rare long-distance dispersal can explain the mismatch between observed plant migration rates (50-13000 m/yr; e.g. Plummer and Keaver 1963, Mack 1981, Delcourt and Delcourt 1987, Birks 1989) and ecological spread models (1-50 m/yr; e.g. Skellam 1951, Chapter 3). Using a mixture of Weibull distributions to simulate dispersal, I predicted a modal spread rate for *Pinus pinaster* moving across fynbos landscapes of 160 m/yr and maximum spread rates of over 750 m/yr. This study adds to the evidence that rare long-distance dispersal events are the key to understanding rapid plant migration (Moody and Mack 1988, Dyer 1995, Shigesada et al. 1995, Ibrahim et al. 1996, Malanson and Armstrong 1996, Clark et al. 1998, Le Corre et al. 1997, Malanson and Cairns 1997, Clark 1998, Cain et al. 1998). Previous models of plant migration have not, with the exception of Clark et al. (1998) and Clark (1998), used data to parameterise their long-distance dispersal functions (e.g. Moody and Mack 1988, Schwartz 1992, Dyer 1995, Collingham et al. 1996, Malanson and Armstrong 1996, Malanson and Cairns 1997). Although these models are potentially useful if parameterised, methods for parameterising their dispersal functions were lacking. Many of these models conceptually used a mixture modelling approach in that they simulated local and long-distance dispersal separately. In this paper I showed how mixture models could be used to statistically describe frequency distributions of dispersal distances, particularly the rare long-distance component of these data sets. Mixture models have the added advantage that their integration into spatial simulation models is simple. This means that the interactions between dispersal, life history, disturbance and landscape structure can be investigated explicitly.

The results showed that spread rates slowed considerably in fragmented systems. This is in agreement with general findings (Gardner et al. 1991, Malanson and Cairns 1997). The predicted spread rates of the model that assumed only local dispersal and the model that included rare long-distance dispersal both decreased linearly with increasing levels of fragmentation. Although both models responded in the same way they did so for different reasons. The local dispersal model showed a linear response to fragmentation because the spread rate was slow relative to the size of the fragments; as fragmentation levels increased the chances of a population encountering unsuitable habitat and stopping increased. The more rapid rate of spread predicted by the models that included rare long-distance dispersal events meant that unsuitable habitats were encountered more often. But the ability to leap across unsuitable habitat ensured that rapid spread continued in moderately fragmented landscapes. However, as fragmentation levels increased, the average distance to suitable habitat increased, while the size

of the founder population decreased. This meant that the likelihood of achieving a successful leap is reduced. What also emerged clearly from this analysis was that long-distance dispersal is likely to interact strongly not just with fragmentation patterns but with plant life-history attributes and disturbance regimes. This is because populations that produce more seeds are more likely to produce more long-distance dispersal events and hence more successful colonists. These results suggest that when rare long-distance dispersal is involved, fragmentation will only reduce the probability of successful migration across a fragmented landscape. This is in agreement with field studies that show that colonisation rates decrease linearly with increasing isolation of islands (Kadmon and Pulliam 1995). It therefore seems that the search for thresholds of landscape connectivity (Gardner et al. 1989, With 1997) is unlikely to be of practical value in predicting migration rates for wind dispersed plants. More testing is needed to tell whether this is a general phenomenon of plant migrations, or all migrations that involve long-distance dispersal. It may be argued that the spread of any population will stop for some configuration of landscape connectivity and this is evidence that thresholds of landscape connectivity do exist. However, these results suggest that the spread rate of species equipped with a rare long-distance dispersal mechanism will gradually decline to zero as the landscape configurations that prevent spread are approached. The radically higher colonisation ability predicted under assumptions of rare long-distance dispersal means that the generality of models in which dispersal mediates species coexistence and persistence in structured landscapes (Tilman et al. 1994, Kareiva and Wennergren 1995) should be re-evaluated.

The exploration of existing data sets and simulated data sets showed that most existing data sets are likely to be inadequate for parameterising long-distance dispersal functions. Statistically the problem is that the central tendency and the tail of a dispersal data set may vary independently (Green 1983, Greene and Johnson 1995). Since the central tendency and not the tail direct the convergence of a maximum-likelihood algorithm, the biologically important part of the distribution has little impact on the model's fit. This analysis showed that more than one model gave a statistically significant fit to a data set. The Akaike Information Criterion is generally recommended for selecting the most parsimonious statistical model (in this case selecting a two-component dispersal model above a three- component dispersal model). This practice results in the trading of biological information for degrees of freedom. These results suggest that methods for collecting dispersal data need to be revised with the awareness that observations of long-distance dispersal are valuable and should not be regarded as noise. In particular, the practice of concentrating on local seed dispersal (Howe and Smallwood 1982) while ignoring the biologically important long-distance dispersal events (e.g. Willson 1993) needs

to be questioned. On the contrary, explicit effort should be dedicated to sampling rare events. These simulations suggest that an order of magnitude of extra sampling effort will often be needed to accurately estimate the long-distance dispersal component. However, these results suggest that relatively large estimation errors are unlikely to strongly influence the predicted spread rate. This latter observation suggests that accurate characterisation of the long-distance dispersal component is not as important as its identification.

The approach demonstrated here remains limited by the inadequacy of existing data and statistical methods. In addition, data on rare long-distance dispersal events will remain (by definition) hard to come by even if considerable effort is dedicated to their collection. Other data sources will have to be considered. For instance recent studies have shown that rare colonisation events can leave a genetic imprint on the spatial structure of populations that can persist for a thousand generations (Ibrahim et al. 1996, Le Corre et al. 1997). Analysis of the spatial structure of these patterns could be used to infer the frequency of long-distance colonisation events. The distance of colonists from seed sources in old field succession situations and the distance of environmental and agricultural weeds from plantations are other possible data sources that could be exploited. Advances in high resolution remote sensing and image processing (Hope 1995) could make the collection of data on the distribution of colonists possible at large spatial extents. The pattern analysis of these data sets is also likely to be useful. Disjunct plant distributions may imply that rare long-distance dispersal is involved, while continuous distributions imply that only short-distance dispersal is involved (Davis 1987, Woods and Davis 1989, Shigesada et al. 1995). Models based on the aerodynamics of seed flight (e.g. Andersen 1991, Greene and Johnson 1995, Hensen and Muller 1997) if linked to extreme value distributions of wind velocity (see Gaines and Denny 1993) could provide another source of information on long-distance dispersal. Showers et al. (1989) showed the potential of this approach by identifying the meteorological events that caused long-distance dispersal of moths.

While the above statements suggest that further progress will only be made once more data is stoically collected, it is clear that modellers need to revisit the natural history of long-distance dispersal. Many mechanisms for long-distance dispersal exist and few have been formally integrated into models. These mechanisms go beyond the traditional candidates for long-distance dispersal such as vertebrate dispersal (vander Wall and Balda 1977, Johnson and Adkisson 1985), water dispersal (Waser et al. 1982, Schneider and Sharitz 1988), tumble-plant dispersal (Mehlman 1993), dispersal by storm winds or updraughts associated with fire (Wheland 1986, Davis 1987, Greene and Johnson 1995), secondary dispersal over the substrate (Bond 1988,

Matlack 1989, Greene and Johnson 1997), and dispersal by secondary agents (Reichman 1984, Kerley 1991). More unusual mechanisms include seed dispersal by raptors that forage on granivores (Dean and Milton 1988); this can result in herbaceous species (unlikely candidates for long-distance dispersal) moving distances greater than 50 km (Lloyd et al. 1998). A similar but more macabre long-distance dispersal mechanism is the decapitation of granivorous birds by telephone lines (P. Lloyd pers. comm.). Similarly Wilkinson (1997) argued that wind-dispersed seeds may often be moved considerable distances by birds. In addition to these freak events, the importance of lesser-known dispersal syndromes should be explored. For example, a suite of species have seeds which appear adapted to dispersal as nest material by birds (Dean et al. 1990); this results in some fairly unlikely seeds being dispersed considerable distances. Another obscure long-distance dispersal mechanism is dispersal by resin-collecting stingless bees (Wallace and Trueman 1995).

CONCLUSION

The seeds of a single plant population will often be moved by a variety of processes. Mixtures of different statistical distributions provide a useful framework for integrating the heterogeneous fates of seeds. The prediction of migration rates requires an integration of the modelling of germination, growth, reproduction, dispersal and mortality in the context of disturbance, plant interactions and landscape fragmentation (Davis 1987, Pitelka 1997). Integrated models capable of simulating these processes have existed for some time (e.g. Pacala et al. 1996, Collingham et al. 1996, Malanson and Cairns 1997, Chapters 3 and 4) and recent contributions have developed useful methods for parameterising the dispersal functions of these models from field data (e.g. Ribbens et al. 1994, Clark 1998, this study). The techniques are in place for making better predictions of which species will arrive when and where. Failure to include long-distance dispersal in migration models is likely to yield qualitatively different predictions. The fact that our knowledge of the pervasiveness of long-distance dispersal is limited means that we do not know when this risk of error high.

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VALIDATION OF A SPATIAL SIMULATION MODEL OF A SPREADING ALIEN PLANT POPULATION

Abstract. Process based models, and spatially explicit models in particular, are likely to play an important role in predicting the impacts of future environmental change. Enthusiasm for the rich potential of these models is however tempered by the realisation that their parameterisation is often challenging and time consuming. Moreover, these models are seldom validated; this makes their predictive value questionable. In this chapter I describe the process of parameterising and validating a spatial demographic model of a spreading alien plant population. The model, a spatially explicit individual-based simulation, has modest data requirements; it concentrates on simulating recruitment, dispersal, mortality and disturbance and ignores the environmental and biotic heterogeneity of the receiving environment. I collected replicated data on the spatial demography of two invasive species and used independent aerial photograph records for the period 1938 to 1989 to reconstruct the invasion histories of two tree species (*Acacia cyclops* and *Pinus pinaster*). The model was parameterised using the demographic data and initiated with a digitised interpretation of the 1938 distribution of alien plants(derived from aerial photography). The observed rates and patterns of invasion, as described by seven response variables, fell within the range of model predictions made at all six sites studied. This approach could be useful as a rapid protocol for parameterising and validating models capable of predicting the spread of plant populations. Moreover, the validated model generates confidence to use the model to explore a variety of applied questions.

Keywords: Spatial models, predictions, invasion biology, error analysis, parameter estimation, *Pinus pinaster*, *Acacia cyclops*.

INTRODUCTION

Growing concern over our ability to manage biota in the face of global change is pressurising ecologists to improve their capacity to make predictions. The rich potential of spatial simulation models to simulate a variety of processes has seen them emerge as the leading paradigm for predicting environmental change. Analytical models, although unquestionably valuable in a strategic context, are unlikely to provide context specific predictions; and statistical models, as

championed by Peters (1992), will be of limited value given the novelty of many of the anticipated environmental changes. However, spatial simulation models are not a panacea, particularly because they can be exceedingly difficult to parameterise (Doak and Mills 1994, Wennergren et al. 1995, Ruckelshaus et al. 1997). Generating confidence in process models is not straightforward: ecological systems are complex, and modelling them involves parameter estimation, assumptions, abstractions and aggregations (Loehle 1987). This means that a modeller could make a great number and many types of errors in constructing a mechanistic model. It follows that the validation stage in the modelling process is crucial for generating confidence in the model's behaviour. This is especially true if the model is to be used as a decision tool (Gentil and Blake 1981). The validation of models is, however, often complicated by the fact that suitable data for validation are not always available and the type of data available varies. Moreover, criteria for validation must be defined in the context of the model's purpose (Rykiel 1996). This means that novel techniques must often be explored in the validation process. In this chapter I develop a protocol for validating a simple spatial simulation model. This protocol is demonstrated using the invasion of South African fynbos ecosystems by two alien tree species, *Pinus pinaster* and *Acacia cyclops*.

Predicting the rates and patterns of plant range expansions is a key issue in invasion biology, conservation biology and global change research. The ability of plants to arrive at and colonise sites is of critical importance for maintaining biodiversity in landscapes (Tilman 1997); for determining the invasive success of alien organisms (Williamson 1996); and for determining the ability of organisms to respond to global climate change (Pitelka 1997). Despite the obvious and critical importance of making predictions about the colonisation potential of plants, very few models of plant spread exist (Chapter 2). In previous chapters I developed a spatially explicit individual-based simulation (SEIBS) model for predicting rates and patterns of alien plant spread (Chapters 3, 4, 5). The philosophy of the SEIBS model was to develop a flexible modelling approach that could incorporate the key processes that determined the spatial population dynamics of invading plant species (Chapter 4). A fundamental component of this modelling philosophy was to operationalise these key processes in functions that could be easily parameterised from field data. The first objective of this chapter is to describe the methods for collecting the field data and show how these data can be used to parameterise the SEIBS model. The second and more fundamental objective is to validate the SEIBS model. Most spread models have been verified by comparing the predictions they make to post-glacial spread rates (Skellam 1951, Cain et al. 1998, Clark 1998). I know of none that have been validated using totally independent data from modern invasions. Contemporary invasions provide a source of data for testing these models, albeit at a finer grain and more limited spatial and temporal extents. The scale

and resolution of contemporary invasion data means that a detailed comparison of the predictions of the spread model and empirical data is possible.

METHODS

The invasion of *Pinus pinaster* and *Acacia cyclops* into unmodified fynbos ecosystems was used as a case study. The process of invasion (Richardson et al. 1992) and the ecological and economic impacts of alien plants (Higgins et al. 1997) in fynbos have been well documented. Fire drives both the natural dynamics of fynbos ecosystems and the invasion of alien plants into these systems. Fires cause widespread mortality of adult plants and provide opportunities for recruitment; and successful alien invader plants compete aggressively for post-fire recruitment opportunities despite suffering high levels fire-induced mortality.

The SEIBS model and its assumptions have been described elsewhere (Chapters 3, 4, 5) and I describe only the details that are relevant to this application. The model simulates the processes of fire spread, plant mortality, recruitment and seed dispersal in a two-dimensional grid. An annual time step is used. Based on the potential sizes of *Pinus pinaster* and *Acacia cyclops* individuals, the model uses grid cells sizes of 100 m^2 for *P. pinaster* and 25 m^2 for *A. cyclops* simulations. The number of recruits that a mature individual can produce is assumed to be a function of its size. The probability of surviving a fire is also assumed to increase with size. The dispersal of recruits is simulated using a mixture of Weibull distributions and the assumption that the dispersal direction is uniform. The probability of fire ignition is assumed to increase as a function of vegetation age. Fire spreads in a spatially explicit manner across the landscape; older vegetation is assumed to have a greater probability of burning.

Parameter estimation

A sensitivity analysis of the model (Chapter 3) showed that it was most sensitive to the dispersal, fire frequency, age of reproductive maturity and recruitment potential parameters; the probability of surviving a fire was less important. These results meant that since good data on fire frequency and of reproductive maturity exist, data collection effort should be directed towards improving the fecundity and dispersal functions.

Acacia cyclops and *Pinus pinaster* reach reproductive maturity after 3 and 6 years respectively. Good data on the fire return intervals in fynbos (typically 8 to 25 years, van Wilgen 1987) means that the probability of ignition (p_i) can be defined as,

$$p_i = \frac{1}{1+\exp(f-a)} \quad (1)$$

where f is a constant that defines the fire return interval and a is the vegetation age.

I used Ribbens et al.'s (1994) RECRUITS method for estimating the recruitment and dispersal potential of adult trees. RECRUITS uses maps of adult trees and recruits to estimate, using maximum likelihood, the fecundity of adult trees and their dispersal ability. RECRUITS assumes that the distribution of recruits in a stand of trees can be related to the fecundity and location of adult trees. RECRUITS predicts the number of recruits (R) produced by a tree of size *dbh* at a location m meters away as

$$R = \left[STR\left(\frac{dbh}{s}\right)^2 \right] \frac{1}{n} \left[e^{-dm^3} \right] \quad (2)$$

where d is the dispersion parameter; STR is the number of recruits produced by a tree of standard size s (s was set to 10 for this study); and n is a normaliser that ensures that the area under the distribution equals 1 (Ribbens et al. 1994).

Adult trees of reproductive size were mapped in belt transects ranging in size from 150x50 m to 300x200 m. Stands that had been burnt in the previous season were mapped since recruitment in fynbos is confined to the immediate post-fire period (Chapter 3). The diameter at breast height and the relative spatial co-ordinates of each adult tree were recorded. I use *dbh* as an index of the trees relative reproductive output. The number of recruits in contiguous quadrats located in the centre of each transect were counted. Recruits were seedlings that had emerged and established after the fire. Six independent transects for each species were measured in a range of sites characterised by different fynbos communities (Table 1). Working in recently burnt stands allowed the estimatation of the probability of fire-induced tree mortality. I recorded whether each mapped tree was dead or alive. These data were used to fit a sigmoidal function that described the probability (P_s) of fire survival as a function of tree size:

$$P_s = l + \frac{(u-l)}{1+\exp\left(\frac{k-dbh}{v}\right)} \quad (3)$$

where *l* is the probability of a tree less than *dbh k* surviving, and *u* is the probability of a tree greater than *dbh k* surviving; *v* is a constant that describes the slope between *l* and *u*. The dispersal parameter estimated using RECRUITS was only likely to be adequate for describing local dispersal (Ribbens et al. 1994). Rare long-distance dispersal events are critically important in invasions and plant migration (Clark et al. 1997, Chapters 3 and 5). For pine trees invading fynbos, gale force winds are likely to disperse pine seeds considerable distances. While most *Acacia cyclops* seeds are likely to be short distances by passive means, birds disperse some seeds much further (Glyphis et al. 1981). A mixture of distributions can be used to describe the stratified nature of dispersal. A mixture of Weibull distributions can be described as

$$g(x) = p_1 b_1 c_1 (b_1 x)^{c_1 - 1} \exp\left\{-(b_1 x)^{c_1}\right\} + \ldots + p_k b_k c_k (b_k x)^{c_k - 1} \exp\left\{-(b_k x)^{c_k}\right\} \quad (4)$$

where p_i is the proportion of recruits, b_i is the scale parameter and c_i is the shape parameter of the i^{th} component of the mixture. Chapter 5 describes the processes of fitting mixture models to dispersal data sets. While Chapter 5 could accurately estimate the local dispersal components for *Pinus pinaster*, it could only estimate probable parameterisations of the long-distance dispersal component. Two conclusions drawn in Chapter 5 guided the definition of a dispersal function. First, data on rare long-distance dispersal will remain (by definition) hard to come by. Second, the rare long-distance dispersal component of the mixture model can be estimated independently of the local dispersal components. For this study I use the RECRUITS data, the *Pinus pinaster* mixture modelling study (Chapter 5), and data on dispersal of *Acacia cyclops* seeds by birds to define a range of possible mixture models. I use the vector $(p_1, p_2, p_3; b_1, b_2, b_3; c_1, c_2, c_3)$ to describe the parameters of a three-component mixture of Weibull distributions.

Both the mortality and recruitment functions use stem diameter. I collected data on the size – age relationship of *Acacia cyclops* by measuring the diameter of trees in even-aged stands of various ages. Published data on the size – age relationship for *Pinus radiata* (von Gadow 1983) were used for *Pinus pinaster*. These data were used to estimate stem diameter (*dbh*) as a function of age (*a*),

$$dbh = m\left(1 - e^{-ra}\right) \quad (5)$$

where *m* is the maximum diameter and *r* is the growth rate.

Table 1. Description of the study sites used for parameter estimation and aerial photograph interpretation for *Pinus pinaster* (P) and *Acacia cyclops* (A). More detailed descriptions of these sites can be found in the corresponding references

Site	Sp	Vegetation	Substrate	Parent material	Rainfall (mm/yr)	Ref.#
			Parameter estimation sites			
1	P	Proteoid fynbos	Colluvial acid sands	Sandstone	600-700	1
2	P	Proteoid fynbos	Colluvial acid sands	Sandstone	600-700	1
3	P	Ericaceous fynbos	Colluvial acid sands	Sandstone	700-800	1
4	P	Ericaceous fynbos	Colluvial acid sands	Sandstone	700-800	1
5	P	Acid sand proteoid fynbos	Leached, infertile sands	Sandstone	450-550	2
6	P	Acid sand proteoid fynbos	Leached, infertile sands	Sandstone	450-550	2
1	A	Mesic oligotrophic proteoid fynbos	Shallow acid sands	Sandstone	800-900	3
2	A	Restiod fynbos	Shallow, neutral, seasonally inundated sands	Limestone	400-500	2
3	A	Restiod fynbos	Shallow, neutral, seasonally inundated sands	Limestone	400-500	2
4	A	Restiod fynbos	Shallow, neutral seasonally inundated sands	Limestone	400-500	2
5	A	Mesic oligotrophic proteoid fynbos	Shallow acid sands	Granite	800-900	3
6	A	Mesic oligotrophic proteoid fynbos	Shallow acid sands	Granite	800-900	3
			Aerial photograph sites			
Elim	P	Acid sand proteoid fynbos	Leached, infertile sands	Sandstone	450-550	2
Caledon	P	Proteoid fynbos	Shallow, leached sands	Sandstone	600-700	1
Napier	P	Proteoid fynbos	Shallow, leached sands	Sandstone	400-500	1
Genadendal	P	Proteoid to ericaceous fynbos	Colluvial acid sands – leached, shallow podzols	Sandstone	700-1500	1
Gansbaai	A	Dune asteraceous fynbos	Unconsolidated calcareous sands	Marine sediments	500-600	2
Hawston	A	Pioneer herbland and open shrubland	Unconsolidated calcareous sands	Marine sediments	600-700	4

1: Campbell 1986, 2: Cowling et al. 1988, 3: Cowling et al. 1996, 4: Lubke et al. 1997.

Aerial photographs

The spatial distribution of *Pinus pinaster* and *Acacia cyclops* were interpreted from historical aerial photographs (1938,1961,1973,1989). I selected sites where cover was low in 1938 and where evidence of human disturbance was low. This proved more difficult for *Acacia cyclops* as it tends to invade the more transformed lowlands (Chapter 7). The areas mapped ranged from 9 km^2 to 16 km^2. The scale of the available photographs varied from 1:30000 to 1:50000; all the photographs were enlarged to an approximate scale of 1:5000. This scale was suitable for the identification of adult trees. Each photograph was geo-referenced by matching features to orthophotos and projected. The interpreted photographs were digitised. The digitised images were converted into raster coverages, which were converted to ASCII files for analysis (see below). Arc/Info (1995) was used for these procedures.

Indices of rate and pattern of spread

A range of spatial indices can describe the rate and pattern of plant spread. (1) *Plant density*: the aerial cover of plants in the site. (2) *Box dimension*: the slope of a log-log least-squares linear regression of the number of boxes with sides of size *h* needed to cover the plant

distribution versus h (Maurer 1994). Using least-squares regression was reliable (r^2 values generally exceeded 0.97). The box dimension is small for complicated and dispersed patterns, but approaches 2 for solid patterns with smooth boundaries. (3) *Mean neighbour distance:* the mean distance of the nearest neighbour from each plant. (4) *SD neighbour distance:* the standard deviation of this nearest neighbour distance. (5) *Mean number neighbours:* the mean number of neighbours in the 8 cells surrounding each plant. (6) *SD number neighbours:* the standard deviation of the number of neighbours. (7) *Dispersion:* a nearest neighbour index that corrects for the effects of plant density (not a variance to mean ratio). The dispersion index (D) is,

$$D = 2\left(X_n \sqrt{d_p}\right)$$

where X_n is the mean neighbour distance and d_p is the plant density.

Validation statistics

Two complementary approaches are used to validate the spread model. First, I evaluate how the data differ from the model's predictions of the seven response variables. Second, I test the level of spatial agreement between the model and the data by doing a cell by cell comparison of the model and data. The agreement is evaluated using a deviance measure and the significance of the agreement is evaluated using a permutation test.

Each sequence of historical aerial photographs used in this study is only one possible realisation of how the invasion sequence could have progressed. Variations in climatic conditions, fire history, and anthropogenic disturbance history mean that many possible invasion sequences could have developed at each site. Because of the observed variation in parameter estimates, there are many possible and valid parameterisations of the model. One way of validating the model is to ask whether the observed data falls within the range or confidence limits of the model predictions. Loehle (1997) advocates a similar approach but asked whether the model's predictions fall within the confidence limits of the data. The danger with this approach is that if the range of parameterisations is very wide, thenthis has low power and will suggest agreement when there is none. This problem can be avoided by changing the definition of agreement by using a variety of confidence intervals. Following Loehle (1997) I develop a test statistic (T) that counts the number of times the data fall within the bounds of the model predictions. The definition of these bounds is varied from the 95 % confidence intervals to the entire range of model predictions. T is estimated for each of

the response variables recorded from the model; a composite test statistic $T' = T/7$ summarises the model's fit across all seven response variables.

The above tests enable us to determine how well the model predicts the rate and pattern of spread. These tests tell us very little about how the model predicts the exact locations of alien plants. I develop a simple permutation test that allows us to ask whether the spatial distribution of the model differs from that of the data, i.e. I test the null hypothesis that the distributions of the populations are the same. A permutation test has the advantage that it makes no assumptions regarding the underlying distributions of the populations being compared (Manly 1991). I use a test statistic *A*, which is the sum of the absolute differences between the model and the data,

$$A = 1 - \frac{\sum |d_{ij} - m_{ij}|}{n} \qquad (6)$$

where d_{ij} and m_{ij} are the population densities at location *(i,j)* for the data and model respectively and *n* is the number of sites. By randomly permuting (1000 permutations were used) the spatial locations of model predictions, it is possible to estimate a distribution for the test statistic *A* and hence the significance of the test (Manly 1991). The spatial grain at which the data is compared to the model will influence the agreement (Costanza 1989). A fine-grained comparison is likely to indicate a poorer agreement between data and model than a coarser grained comparison. For this reason I use the concept of a multiple resolution procedure (Costanza 1989) and repeat the test for a range of spatial grains from 10000 m^2 to 50000 m^2.

RESULTS

Parameter estimation

The recruitment and dispersal parameter estimates are shown in Table 2. Estimates of recruitment potential (*STR*) for *Pinus pinaster* ranged from 1-15 recruits per adult of 10 cm dbh. The lower and upper confidence limits of this range were 0.68 and 28.34 respectively (Table 2). Estimates of mean dispersal distance (*MDD*) ranged from 4 to 30 meters. The confidence limits of the *Acacia cyclops STR* estimates ranged from 3 to 89; and the *MDD* estimates ranged from 3 to 10 m (Table 2). The fitted sigmoidal function describing the probability of a stem

Table 2. Parameter estimates for the RECRUITS model. STR (Standard total recruitment), d and normaliser (Equation 1) for six sites invaded by *Pinus pinaster* and for six sites invaded by *Acacia cyclops*. MDD (mean dispersal distance) is presented as a more intuitive interpretation of d. Each site is an independent replicate and the correlation between data and the RECRUITS model prediction were significant ($p<0.05$) for all sites.

Site	*STR*	Low CI *STR*	High CI *STR*	*d*	*MDD*	Low CI *MDD*	High CI *MDD*	Normaliser
				Pinus pinaster				
1	3.0755	2.2784	4.0410	0.0061012	4.03835	3.3786	4.9370	85.0039
2	5.0822	3.3366	7.3319	0.000017112	28.6574	22.9751	36.1774	4270.9189
3	4.1504	3.0087	5.5578	0.0061918	4.0185	3.0660	6.6082	84.1730
4	6.0808	4.7040	7.7139	0.00028802	11.1787	6.4862	16.8093	640.04934
5	14.7099	6.2992	28.3424	0.000021783	26.4220	18.5724	43.0989	3636.1872
6	1.0582	0.6839	1.554	0.000014401	30.3534	22.7652	40.7824	4791.3867
				Acacia cyclops				
1	3.8580	3.3875	4.328	0.0011686	7.0092	6.1230	8.6612	255.6877
2	24.2514	16.7972	33.6640	0.011241	3.2928	2.7480	3.9676	56.58104
3	40.3662	29.9845	52.8624	0.002613	5.3589	4.5477	6.4952	149.5388
4	61.3056	52.6248	70.7836	0.01410	3.0527	2.3336	3.7321	48.6601
5	20.2871	15.6373	25.8524	0.0009765	7.4420	6.2324	9.3133	288.2057
6	78.4298	69.1909	88.5782	0.0006661	8.4544	7.3186	9.8629	371.8945

surviving a fire as a function of stem dbh (Equation 3) was $P_s = 0.0441 + (0.0819\text{-}0.0441) / 1 + \exp(10.784\text{-}dbh)/1.060$ ($R^2 = 0.685$) for *P. pinaster*. No relationship between stem size and probability of mortality was found for *A. cyclops*. Consequently the frequency of tree survival was used to estimate the probability of fire survival ($P_s = 0.0168$ for *A. cyclops*). The fitted parameters of the age-size relationship (Equation 5) for *P. pinaster* were $m = 41.4$ and $r = 0.0669$ ($R^2 = 0.98$); for *A. cyclops* $m = 20.4$ and $r = 0.093$ ($R^2 = 0.745$).

Empirical invasion pattern

The range of spread rates recorded for *Pinus pinaster* and *Acacia cyclops* were very similar, although the range was wide (Table 3). The rate of increase in aerial cover ranged from 3.7 to 6.2 % per year for the four sites invaded by *P. pinaster* and 2.7 to 6.1 % for the two sites invaded by *A. cyclops* (Table 3, Figures 1 to 6). These parameters suggest that it will take 10 to 30 years for the invaded area to double. Since typical fire return intervals are between 8 and 25 years, it will take one or two fires for the area invaded to double. The square root of the area invaded per year can be used to estimate the linear rate of spread (Table 3). These data are reported since spread rates are often reported this way, although these estimates are likely to be biased by the boundary effects. The linear rate of spread as estimated ranged from 17 to 31 m/yr (Table 3).

Table 3. Estimated invasion rates and linear rates of spread for four sites invaded by *Pinus pinaster* and two sites (Gansbaai and Hawston) invaded by *Acacia cyclops*. Invasion rates were estimated using a natural log of area versus time linear regression; linear rates of spread were estimated using a square root of area versus time linear regression.

	Invasion rate				Linear rate of spread (m/yr)			
site	rate	Constant	R^2	P	rate	constant	R^2	p
Elim	0.062	9.398	0.927	0.0370	22.79	-530.5	0.994	0.0028
Caledon	0.034	11.61	0.979	0.0108	17.46	-81.38	0.936	0.0324
Napier	0.043	11.32	0.997	0.0016	24.60	-363.5	0.957	0.0216
Genadendal	0.027	13.71	0.954	0.0235	31.39	341.3	0.938	0.0310
Gansbaai	0.061	9.674	0.987	0.0066	30.60	-907.4	0.897	0.0529
Hawston	0.027	13.08	0.974	0.0129	21.31	-322.78	0.991	0.0045

The pattern of invasion is also similar for both species (Figures 1 to 6). A comparison between the density and box dimension data shows that the box dimension increases with alien density. This means that the distribution of alien plans is more scattered early on in the invasion but becomes more aggregated as the invasion progresses. Clumping only occurred later at two of the *P. pinaster* sites (Figures 2 and 3). The mean and standard deviation of mean nearest neighbour distance tended to decrease as the invasion progressed, again indicating that plant distribution aggregates as the invasion progresses. The same trends can be seen in the mean and standard deviation of number of neighbours data. The mean number of neighbours increased as the invasion progressed, while the standard deviation of the number of neighbours decreased. The dispersion index closely reflected the density data. A correlation matrix between these indices of the rate and pattern of invasion showed that the dispersion index was redundant. The correlations between the other variables, although high, indicated that each variable provided different information (Table 4).

Table 4. Correlations between empirical measurements of invasion pattern over time (1938,1961,1971,1989) at four sites invaded by *Pinus pinaster* (n=16) and two sites invaded by *Acacia cyclops* (n=8).

	p. d.	b. d.	M. n. d.	SD n. d.	M. n. n.	SD n. n.
			Pinus pinaster			
Plant density (p.d.)	1.0					
Box dimension (b.d.)	0.749	1.0				
Mean neighbour distance (M.n.d.)	-0.497	-0.702	1.0			
SD neighbour distance (SD.n.d.)	-0.597	-0.713	0.980	1.0		
Mean number neighbours (M.n.n.)	0.532	0.707	-0.927	-0.920	1.0	
SD number neighbours (SD. n. n.)	-0.698	-0.327	0.543	0.687	-0.514	1.0
Dispersion	0.922	0.729	-0.575	-0.705	0.621	-0.823
			Acacia cyclops			
Plant density	1.0					
Box dimension	0.970	1.0				
Mean neighbour distance	-0.664	-0.742	1.0			
SD neighbour distance	-0.689	-0.753	0.996	1.0		
Mean number neighbours	0.824	0.904	-0.523	-0.520	1.0	
SD number neighbours	-0.685	-0.702	0.946	0.968	-0.408	1.0
Dispersion	0.987	0.987	-0.755	-0.77	0.845	-0.759

Model validation

For the validation runs the model was initiated with the 1938 distributions and the parameters that the model was most sensitive to (recruitment, dispersal and fire frequency parameters,

see Chapter 3) were varied. The age of maturity (the other important parameter identified in Chapter 3) was not varied as this is unlikely to change from site to site for the species considered here. Three levels of each parameter were used in the validation runs (27 factor combinations were run for each site). The parameters used for these runs are listed in Table 5. The range of fire return intervals (*a*) was selected to include fire management regimes that ranged from arson to fire prevention. The recruitment levels (*STR*) represent the ranges recorded in the field (Table 2). The dispersal parameters (p_1,p_2,p_3; b_1,b_2,b_3; c_1,c_2,c_3) were estimated from the parameters estimated in this study, the analysis of evidence for long-distance dispersal in *Pinus pinaster* dispersal data (Chapter 5), and data on dispersal of *Acacia cyclops* seeds by birds (Glyphis et al. 1981). The lower and medium parameter sets assume no long-distance dispersal; the upper parameter estimate includes rare long-distance dispersal events.

Running the model using these empirical parameter estimates showed a good agreement between the model and the data. Figures 1 to 6 show graphically how the model and data agree for each of the sites where an invasion history was reconstructed. In general, the empirical estimates of the indices falls within the range of values predicted by the model. This agreement is explored more formally in Tables 6 and 7 where T' statistics (see methods) are calculated for each site. The agreement between the model and data improves as one move from 1961 through to 1989 (Tables 6 and 7). This suggests that small errors

Table 5. Lower, medium and upper parameter levels used for the validation runs for *Pinus pinaster* and *Acacia cyclops* (*f*=fire return interval[#]; *STR*=standard total recruitment[*]; p_i,b_i,c_i = parameters of a mixture of Weibull distributions used to describe dispersal[+])

Parameter	*Pinus Pinaster*			*Acacia cyclops*		
	Low	medium	upper	low	medium	upper
F	10	15	20	10	15	20
STR	3	15	27	3	40	80
p_1	0.912	0.953	0.953	1	1	0.001
p_2	0.088-	0.047	0.046	0	0	0.999
p_3	0	0	0.001	0	0	0
b_1	0.166	0.0625	0.0625	0.333	0.04	0.04
b_2	0.0238	0.0156	0.0156	-	-	0.002
b_3	-	-	0.0001	-	-	-
c_1	1.778	1.983	1.9825	1	1	1
c_2	1	1	1	-	-	1
c_3	-	-	1	-	-	-

[#]equation 1, [*]equation 2, [+]equation 4.

Table 6. *T'* statistics calculated for 95, 99, 99.9 confidence intervals and for the range of model predictions for four sites invaded by *Pinus pinaster* and at three time intervals. The *T'* statistic counts the proportion of times that the data falls within the confidence interval or range of model predictions.

Site	Elim				Caledon				Napier				Genadendal			
CI	95	99	99.9	range	95	99	99.9	range	95	99	99.9	range	95	99	99.9	range
1961	0.14	0.29	0.43	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.86	0.00	0.00	0.14	0.71
1973	0.14	0.29	0.29	1.00	0.14	0.14	0.14	0.57	0.14	0.14	0.29	0.57	0.00	0.29	0.86	1.00
1989	0.00	0.14	0.86	1.00	0.57	0.57	0.57	0.86	0.43	0.43	0.57	1.00	0.00	0.00	0.57	1.00

characterising the initial conditions, particularly errors in digitising outlying individuals, and not knowing the exact fire history does not result in the propagation of errors; on the contrary these effects tend to average out as the invasion progresses. In some cases this increasing agreement over time may be because stand density is approaching 1: Genadendal (Figure 4) and Hawston (Figure 6) have 1989 densities above 0.7; however, at the other sites the 1989

densities were less than 0.5. The range of predictions is narrower for *Pinus pinaster* than for *Acacia cyclops*. This is because of less variation in the parameter estimates (Table 2). The broader range of predictions for *A. cyclops* suggests that using the confidence limits may be a more appropriate level for model evaluation. The 1989 *T'* statistics are higher for *A. cyclops* at both sites for all confidence levels. For *P. pinaster* sites, the narrower range of predictions means that the model agrees poorly with the data at the 95 % confidence interval level. If the range is used as the definition then agreement in 1989 is absolute for the Elim, Napier, Genadendal, Gansbaai and Hawston sites, and 0.86 for the Caledon site. The relatively poor agreement at the Caledon site is probably due to the failure to predict the distribution of outlying plants (Figure 2).

The results of the tests of the spatial agreement between the model and the data are presented in Figure 7. As expected the general trend shows that as the spatial grain of the analysis increases the agreement between the data and the model improves. The average level of agreement between the model and data is generally above 0.7 and is as high as 0.9

Table 7. *T'* statistics calculated for 95, 99, 99.9 confidence intervals and for the range of model predictions for two sites invaded by *Acacia cyclops* and at three time intervals. The *T'* statistic counts the proportion of times that the data falls within the confidence interval or range of model predictions.

Site	Gansbaai				Hawston			
CI	95	99	99.9	range	95	99	99.9	range
1961	0.14	0.14	0.14	0.71	0.14	0.43	0.72	1.0
1973	0.43	0.43	0.57	0.86	0.86	0.86	1.0	1.0
1989	0.57	0.86	1.0	1.0	1.0	1.0	1.0	1.0

(Figure 7). The agreement using some parameterisations at fine spatial grain are lower than 0.5; but agreement ranges up to 0.97 at coarser grain for some parameterisations (Figure 7). The agreement statistic may be regarded as somewhat biased in the early and late phases of invasion, since a model that predicts the right density at these phases is likely to have a high level of spatial agreement. However, in this case the agreement remains high even at intermediate densities (0.2-0.8, Figures 1-6) suggesting that the high level of spatial agreement (Figure 7) is not an artefact. The permutation test (see methods) aims to assess whether the agreement between the model and data is better than would be predicted by a permuted distribution of invaded sites. Gansbaai was the only site where some parameter combinations did not predict spatial patterns that were not better than random. Eight parameter combinations in 1989 and four parameter combinations in 1973 were not significantly (at the 5% level) better than random. All other sites, at all times, and for all parameter combinations predicted spatial patterns that showed closer spatial agreement to the data than random permutations of the data.

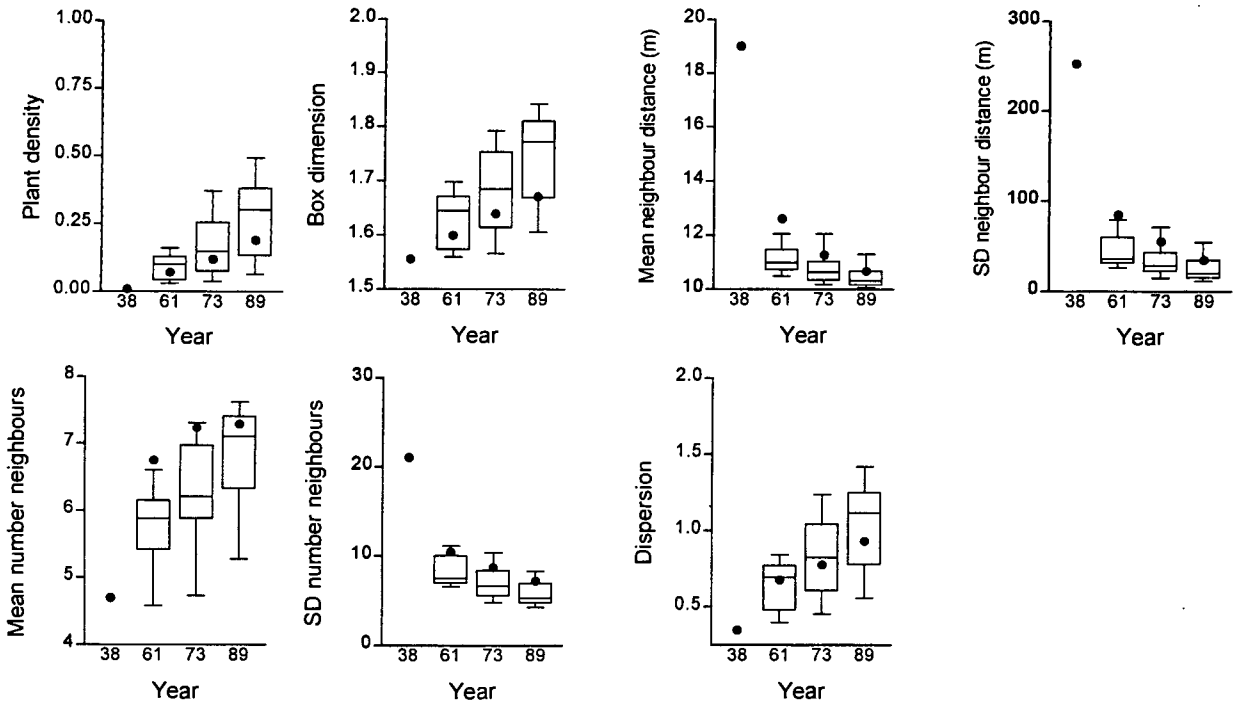

Figure 1. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Pinus pinaster* at the Elim site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

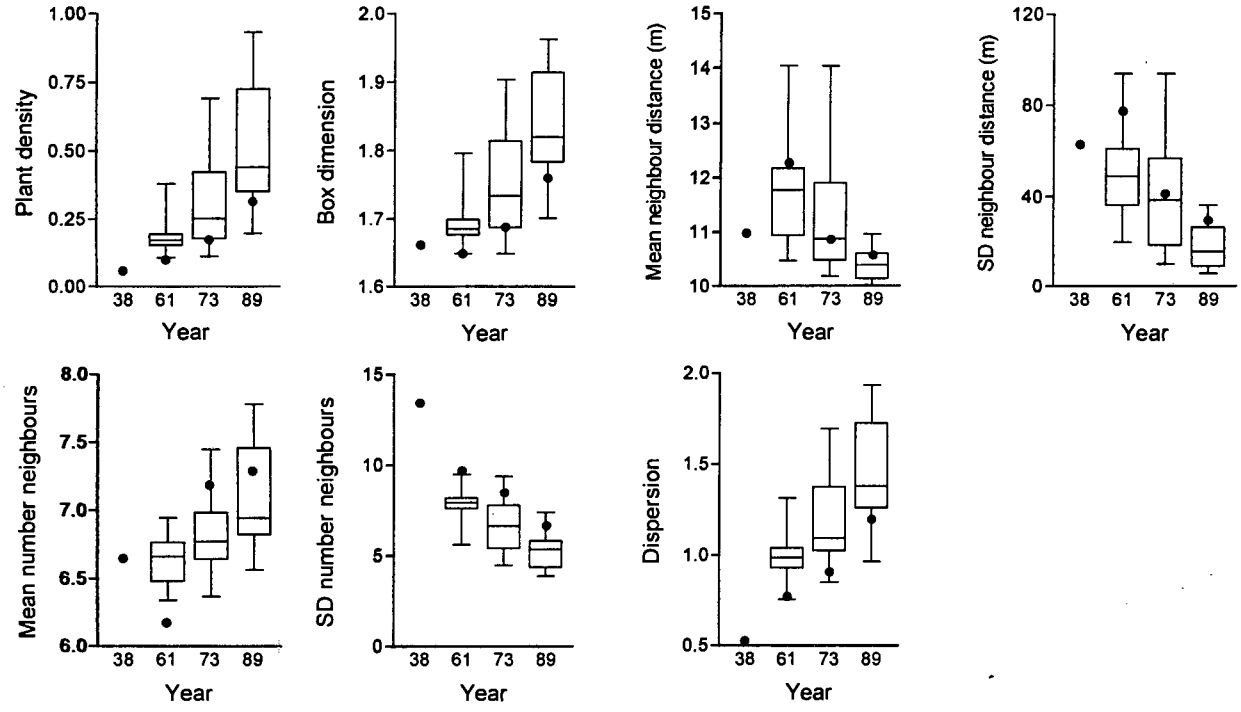

Figure 2. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Pinus pinaster* at the Caledon site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

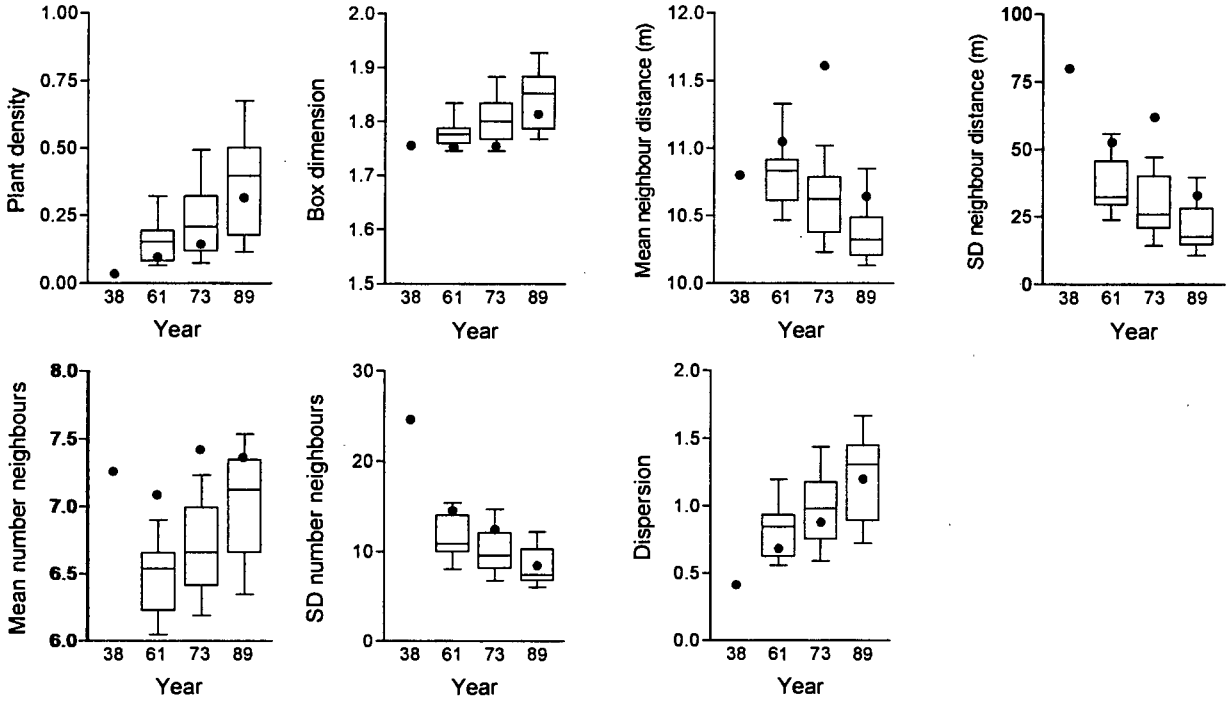

Figure 3. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Pinus pinaster* at the Napier site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

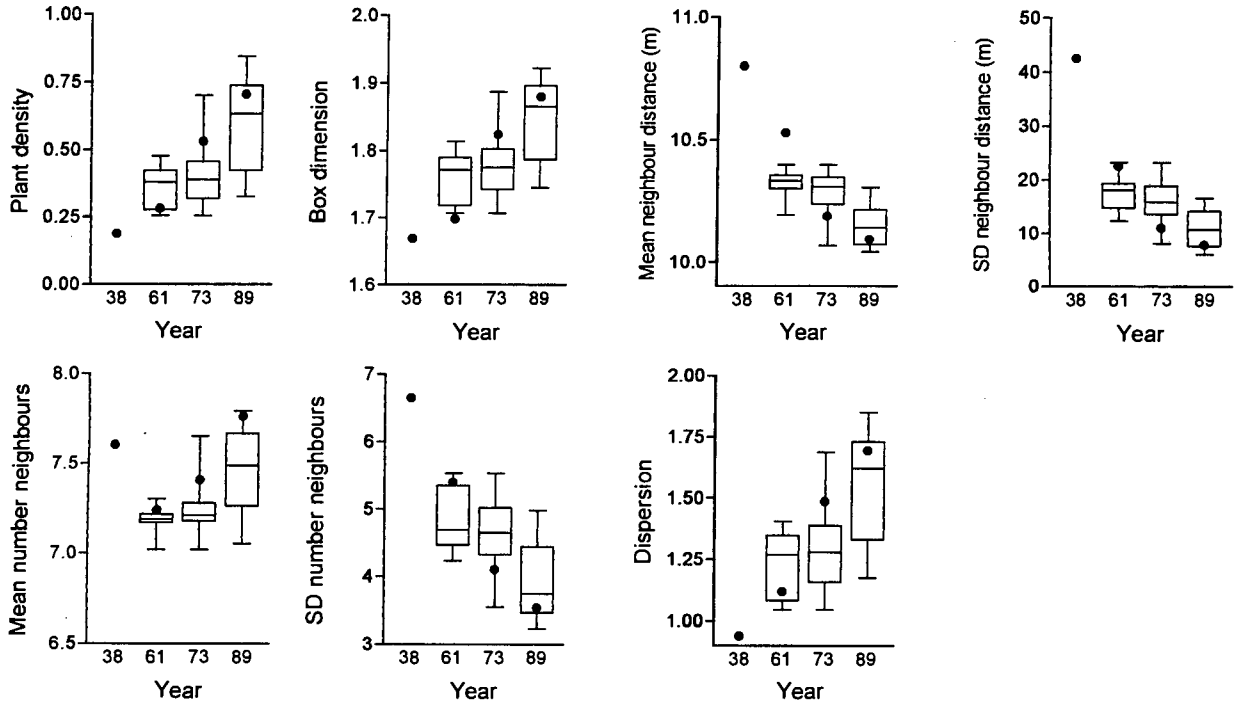

Figure 4. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Pinus pinaster* at the Genadendal site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

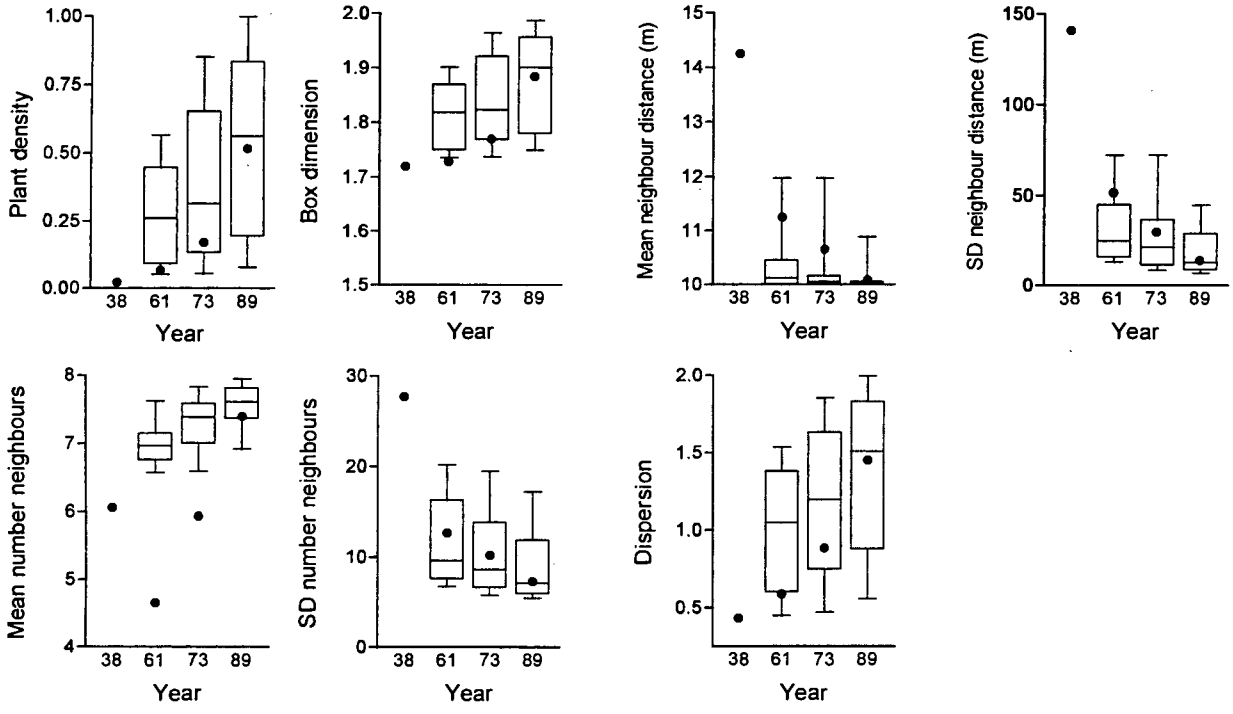

Figure 5. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Acacia cyclops* at the Gansbaai site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

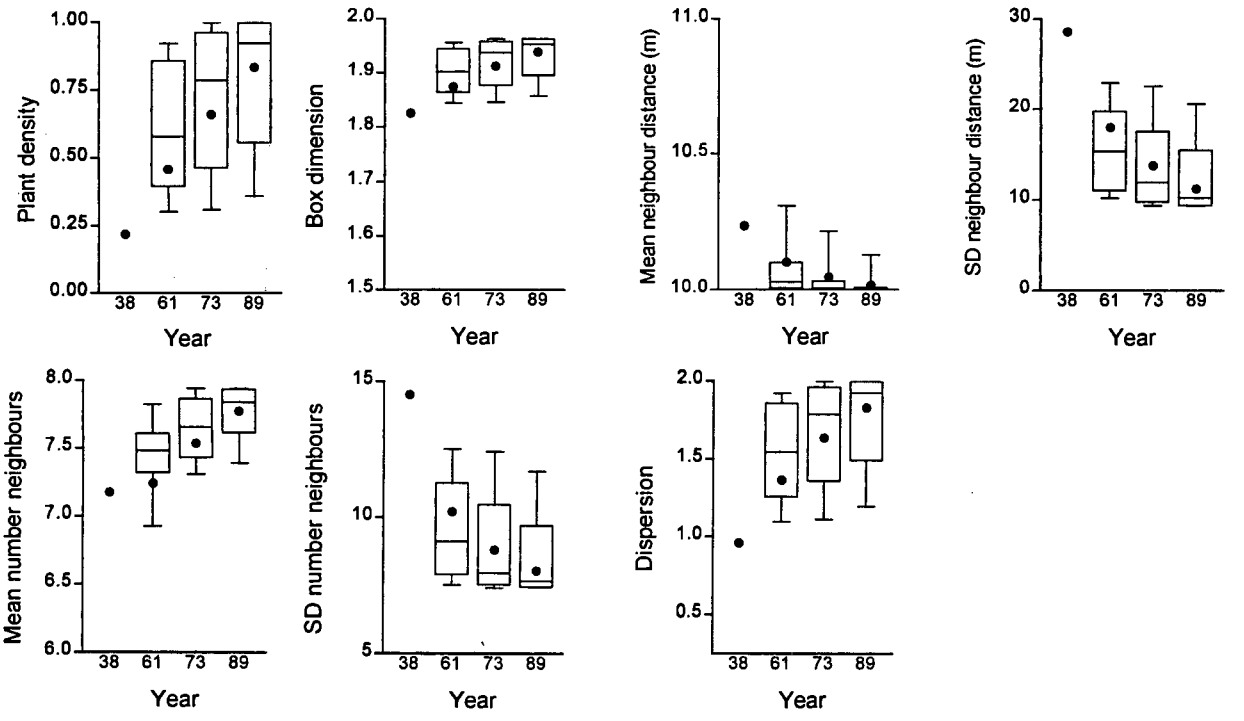

Figure 6. Plant density, box dimension, mean nearest neighbour distance, SD of nearest neighbour distance, mean number of neighbours, SD of number of neighbours, and dispersion for *Acacia cyclops* at the Hawston site in 1938, 1961, 1973 and 1989. Points are the empirical data, box and whisker plots show the range of predictions made by the model using 27 model parameterisations. Model parameterisations were defined by independent field data sampling (Table 5).

DISCUSSION

There are many potential sources of error in ecological models and it is difficult to evaluate all of them explicitly. Important potential sources of error in this study included the assumptions of the size of an individual plant, an absorbing boundary and spatial homogeneity of the environment, no inter-fire recruitment, parameter estimation error and initial condition estimation error. In addition the exact fire histories for the different sites were unknown. Despite these many potential sources of error, the model's predictions agree remarkably well with the observed pattern of invasion at the stand (< 20 km^2) scale; this agreement was robust given the observed variation in independent parameter estimates. This implies that some of the fundamental assumptions the model makes regarding how invasions proceed in fynbos are valid. Importantly, it was assumed that the community composition of the receiving environment does not influence the rates and patterns of invasion at this scale. The sites invaded by *Acacia cyclops* ranged from relatively densely vegetated dune asteraceous fynbos to a low cover headland by-pass dune, whereas the sites invaded by *Pinus pinaster*

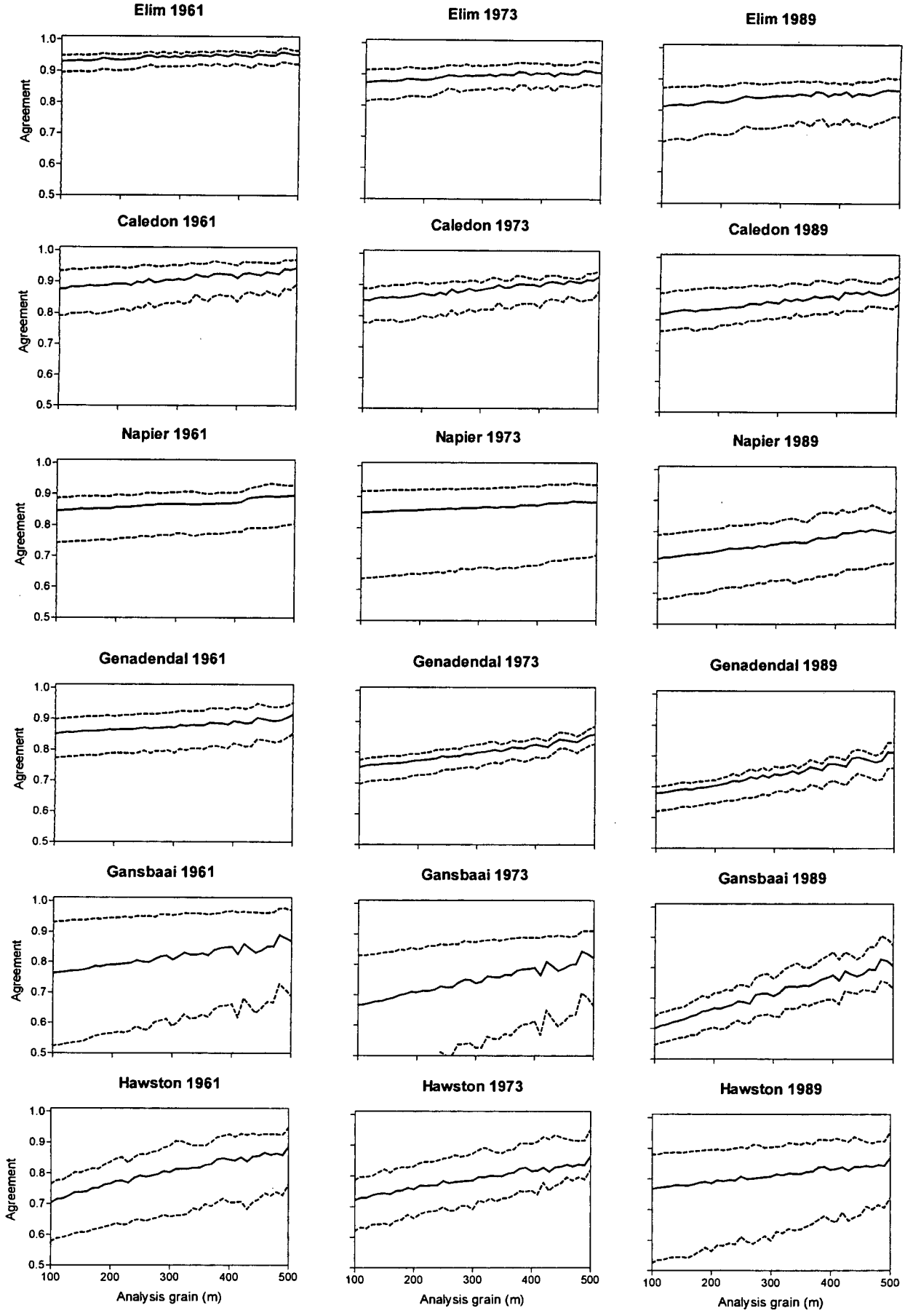

Figure 7. The level of agreement (Equation 2 between the model and data for each of the six sites in 1961, 1973 and 1989 at increasing spatial grain. The solid line is the average level of agreement for 27 model parameterisations; the broken lines are the best and worst agreement of the 27 model parameterisations (Table 5).

ranged from proteoid fynbos (characterised by a proteoid overstorey and heath understorey) to ericaceous fynbos (single stratum). In addition high levels of alpha, beta and gamma diversity within these vegetation types (Cowling 1990, Simmons and Cowling 1996) implies that local species composition would have varied considerably. While the high levels of functional redundancy characteristic of fynbos (Cowling et al. 1994) may explain the limited effect of species composition on invasion rates, the limited effect of structural and soil differences between the sites is intriguing. These results contrast with finer scaled experimental studies that have illustrated that the composition, diversity and nutrient availability of the receiving environment strongly influences invasive success and invasion patterns (Tilman 1997, Stohlgren et al.1998). The limited effect of the receiving environment in fynbos can be attributed to two factors. First, the extreme fecundity of the alien populations makes differences in the invasive resistance of different fynbos communities insignificant (Milton 1989, Honig et al. 1992). Second, the environmental tolerances of fynbos invaders are considerably wider than those of the native species (Richardson et al. 1992, Chapter 7).

The empirical data on the rates of invasion presented here contribute to a growing database on plant invasions. The rates of invasion estimated from historical aerial photographs were between 0.027 and 0.062. This is slower than the invasion rate of *Pinus radiata* in fynbos (0.079, calculated from Richardson and Brown 1986). Forcella (1985) reviewed the spread of 40 alien weed species in north-western United States; invasion rates calculated from his data ranged from 0.0262 to 0.0562 (mean = 0.03953). Other invasion rates found in the literature provide similar estimates: 0.059 for *Ammophila arenaria* invading dunes in California (Buell et al. 1995), 0.042 - 0.110 for a range of species in riparian habitats in the Czech Republic (Pysek 1991), 0.031-0.056 for three *Impatiens* species in the British Isles (Perrins et al. 1993), 0.131 for *Eragrostis lehmanniana* in southern Arizona (calculated from data in Anable et al. 1992) and 0.12 for *Bromus tectorum* in north-western United States (calculated from Mack 1981). However, incredibly rapid invasion rates have also been reported: 0.59 for *Mimosa pigra* in northern Australia (Lonsdale 1993) and 0.701 for *Baccharis pilularis* in northern California (calculated from Williams et al. 1987). Fewer studies report linear rates of spread, and the estimates reported here should be regarded as minimal estimates since rare long-distance events fell outside the scale of this study. This study suggests that *Pinus pinaster* and *Acacia cyclops* spread at 21-31 m/yr; this is slightly slower than *Pinus radiata* invading fynbos (31 m/yr calculated from Richardson and Brown 1986). *Mimosa pigra* spread at 76 m/yr in northern Australia (Lonsdale 1993), and *Ammophila arenaria* spread at 14 m/yr

in California (Buell et al. 1995). Linear invasion rates estimated at continental scales can be more spectacular: Mack's data on *Bromus tectorum* invasion into north-western United States suggests rates of up to 5 km/yr (estimated from Mack 1981); Plummer and Keaver (1963) report spread rates of between 4 and 13 km/yr for *Heterotheca latifolia* invading the Georgia piedmont region. Clearly the scale of the invasion (and the invasion study) strongly influences the reported spread rate. The estimates of *P. pinaster* invasion rates of up to 31 m/yr (reported here) contrast strongly with the 200-500 m/yr predicted by the SEIBS model at an unlimited spatial extent (see Chapter 5). These predicted rates are in the same order of magnitude as post-glacial migration rates of trees (Delcourt and Delcourt 1987, Birks 1989).

There is a tradition of relating pattern to process in ecology. While many studies that use pattern analysis has been criticised for their obscure link to process (Cale et al. 1993), the linking of spatial simulation models to pattern analysis provides a more direct link between pattern and process. This study established such a link and the results suggest that there is considerable potential in relating spatial patterns of invasion to rates of invasions. I found correlation between rates and patterns of spread in both the empirical data and in the simulation model. Similar relationships were found in a simulation study (Chapter 3) and in studies of post-glacial migration of trees (Davis 1987). Since species that spread with a more diffuse pattern tend to spread faster, it may be possible to use pattern analysis of species at their range limits to separate species capable of rapid spread from those that are likely to be slow spreaders. Such an analysis would only be valid if there was evidence that environmental conditions do no limit the species at its range boundary. Achieving this necessitates linking spread models more tightly to models of environmental tolerance than they are at present.

Very few models of the spatial dynamics of plants have been validated. Most authors rely on impeccable parameterisations and sound model construction to generate confidence in their models. This can be dangerous, as good parameter estimates do not guarantee that the key processes are included or correctly modelled. Although the process of parameterising and validating a model can be long and arduous, it remains possible. For example, Pacala and colleagues recently developed and validated a spatial simulation model of forest community dynamics (Pacala et al. 1996). Although this demonstrates what is possible, the resources needed to achieve this will probably cause the more pragmatic and time-limited amongst us to scurry for statistical models. However, the message that emerged from Pacala's work is that effort in parameterising and validating process-orientated models is rewarded with insights

that would be difficult, if not impossible, to obtain using statistical methods (Pacala and Deutchman 1995). However, not every problem needs a detailed and complex model and many problems can be effectively dealt with using simple process-orientated models that have more modest data requirements (e.g. Silvertown et al. 1992, Hanski 1994, Chapter 4). The model presented here, which simulates a few simple demographic processes, shows that spatial models can be simple and rapidly parameterised. The advantage of having this process-orientated model, as opposed to a statistical model of invasion (e.g. Perrins et al. 1993, Pysek and Prach 1993, Londsdale 1993), is that the model can be used, with confidence, to address a range of management questions. For instance the model developed here could be used to predict the most cost-effective alien clearing strategy and the potential impact of alien plants on fynbos ecosystems (Higgins et al. 1997, see Chapter 8).

Even though the parameters estimated could be used to validate the model, this does not mean that the model's behaviour is necessarily robust under all conditions and at all scales. While the coupling between parameter estimation error and model prediction error is likely to vary depending on the model's sensitivity to that parameter (e.g. Ruckelshaus et al. 1997), this sensitivity may only be revealed at certain scales. For instance the validation presented here suggests that any of the dispersal parameterisations used are adequate; however, under severe levels of fragmentation and large spatial scales the inadequacies of some of these parameterisations would be revealed (Chapter 5). This observation further emphasises the critical importance of dispersal in spatial models (Gardner et al. 1991, Ruckelshaus et al. 1997, Chapters 3 and 5). Innovative work will be needed to link stand scale studies to the regional scale in a rigorous framework. For tree and shrub invasions, advances in high resolution imagery are likely to provide useful data on the distribution of recruiting alien plants relative to pine plantations at large spatial extents. These data could be used to validate the dispersal models at a larger spatial extent.

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PREDICTING THE LANDSCAPE SCALE DISTRIBUTION OF ALIEN PLANTS AND THEIR THREAT TO PLANT DIVERSITY

Abstract. Invasive alien organisms pose a major threat to global biodiversity. The Cape Peninsula, South Africa, provides a case study of the threat of alien plants on native plant diversity. I aimed to identify where alien plants would invade in the landscape and what their threat to plant diversity could be. This information is needed to develop a strategy for managing these invasions at the landscape scale. Logistic regression models were used to predict the potential distribution of six important invasive alien plants in relation to several environmental variables. These predictions were overlaid on the current (1994) distribution of native plant diversity for the Cape Peninsula. The results showed that alien plants could cover at least 89 percent of the Cape Peninsula. *Acacia cyclops* and *Pinus pinaster* were predicted to cover the greatest area. The threat to native plant diversity, quantified as the number of plant species; rare and threatened plant species; and endemic plant species with their entire range covered by the predicted distribution of alien plant species was calculated. This showed that *P. pinaster* posed the greatest threat to the plant diversity of the Cape Peninsula. A null model of threat, where invaded sites are randomly selected, showed that most alien species threaten more plant species than would be predicted from the area they invade alone. *P. pinaster* threatens 350 more native species, 29 more rare and threatened species and 21 more endemic species than the null model would predict. The results emphasise the importance of adopting a spatially explicit approach for quantifying threats to biodiversity and provide the information needed to prioritise the alien species and the sites that need urgent management intervention.

Key words: logistic regression, biological invasions, null models, biodiversity threat.

INTRODUCTION

Invasive alien organisms, one of the major threats to global biodiversity (Pimm et al. 1995), impact negatively on all components of biodiversity, from genes to ecosystem processes. This has been documented in case studies from all parts of the world. Alien plants have been shown to increase carbon assimilation rates (Le Maitre et al. 1996), change soil nutrient status (Vitousek and Walker 1989), increase flammability (Anable et al. 1992), threaten native plant

species (Musil 1993, Meyer and Florence 1996) and change habitat suitability for native animal species (Steenkamp and Chown 1996, Allan et al. 1997). Many of these impacts have secondary impacts on ecosystem functioning (Vitousek and Walker 1989). For instance, the increased biomass of alien plants in fynbos ecosystems substantially increases plant water use, which reduces runoff (Le Maitre et al. 1996). The economic consequences of these impacts are substantial (Cowling et al. 1997, Higgins et al. 1997).

Of particular concern for conservation is the invasion of alien plants into unmodified ecosystems since these systems are important repositories of biodiversity. Cape fynbos ecosystems provide an example of a biodiverse system threatened by plant invasions. The Cape flora consists of 8574 species, 62.2% of which are endemic; in addition 19.5% of the 989 genera are endemic (Cowling et al. 1992). An estimated 36% of remaining intact (untransformed by urbanisation and agriculture) Cape fynbos systems are invaded by woody alien plants. Invasion can reduce native plant species richness by 50 to 86% (Richardson et al. 1989, Holmes and Cowling 1997) and can increase the probability of local extinction of a wide range of the functional plant types found in fynbos by 40 to 80% (Musil 1993). These results suggest that alien plants are a substantial threat to the plant diversity of fynbos.

The best way of preventing these impacts is undoubtedly to prevent the introduction of high risk taxa (Tucker and Richardson 1995, Reichard and Hamilton 1997), but it is too late for this in many cases. This means that the best hope of mitigating the impacts of alien plants is through mechanical, chemical and biological control. However, the large scale of the problem means that an informed strategy is needed. Despite the urgent need for such strategies in the face of many types of human threat to biodiversity, few studies have attempted to systematically and quantitatively assess current and future risks to biodiversity at the landscape scale (White et al. 1997). Richardson et al. (1996) attempted to link potential distributions of alien plants with the distribution of biodiversity, but their models of potential alien distribution were qualitative. While Le Maitre et al. (1995) and Higgins et al. (1997) examined scenarios of alien plant spread and threat in fynbos ecosystems, they did not consider the environmental tolerances of the invasive species. This study aims to: (1) develop statistical models which predict the site-specific likelihood of an alien plant species invading; and (2) to overlay these predictions with the distribution of native plant diversity in order to define the distribution of alien plant threat.

METHODS

Study area

The Cape Peninsula covers 471 km^2. The geology of the area is dominated by quartzitic sandstones of the Table Mountain Group which overlay granites of the Cape Granite Suite. These are interspersed with siliceous and calcareous sands in the valleys and coastal bottomlands (Cowling et al. 1996). The topography is dominated by the Peninsula Mountain Chain which runs from Table Mountain (1113m) in the north to Cape Point in the south. The soils are generally sandy and nutrient-poor. The climate is characterised by cool, wet winters and dry, warm summers. Steep rainfall gradients exist on the Cape Peninsula, with annual rainfall ranging from an average of 402 mm at Cape Point to 2000 mm on Table Mountain.

The flora of the Cape Peninsula comprises 2285 vascular plant taxa (2283 species and 2 subspecies); 90 are endemic and 141 are classified as Red Data Book species (Trinder-Smith et al. 1996a). This exceptional species richness is attributed to high turnover of species within and between habitats coupled with steep and long habitat gradients (Simmons and Cowling, 1996).

Data sources

The remaining intact land (32847 ha untransformed by urbanisation and agriculture) on the Cape Peninsula defined the study area (see Richardson et al. 1996). Six alien plant species were selected for the analysis: *Acacia cyclops, A. longifolia, A. mearnsii, A. saligna, Pinus pinaster* and *P. radiata*. These species were selected because they are abundant on the Cape Peninsula and elsewhere in the fynbos biome. They have also been in the area for over 100 years (Richardson et al. 1992, Richardson et al. 1996). The environmental data used were: altitude, slope, solar radiation, annual rainfall, soil fertility index, soil moisture index and flammability index.

Alien plant presence/absence was digitised at a 1:10 000 scale (Richardson et al. 1996). Altitudes were interpolated using Arc/Info (1995) from a digital elevation model built from 50 m^2 resolution data. Slope and aspect were derived from the digital elevation model using standard Arc/Info (1995) functions. Average daily radiation was calculated in cal/cm^2 from slope, aspect and latitude using Swift's (1976) algorithm. Annual rainfall was interpolated using standard Arc/Info functions from rainfall isohyets (1:250 000). Three categories of both soil moisture

and soil fertility were estimated for each of 15 vegetation types (mapped at 1:10 000, Richardson et al. 1996). Four categories of flammability were estimated from the predicted flame lengths of each of the vegetation types (Le Maitre and Marais 1995). All data sets were interpolated to a 50 m^2 grid.

An excellent database of native plant taxa exists for the Cape Peninsula (Trinder-Smith et al. 1996b). This database used 48139 herbarium records to interpolate the distribution, at a 1 km^2 resolution, of native plant species on the Peninsula. The conservation status (rare, threatened and/or endemic) is also recorded for each species. A total of 2093 plant species, of which 124 are rare and threatened and 90 endemic, fall in the study area. For convenience I call Trinder-Smith's (1996b) rare and threatened plants *rare plants* in this study.

Sampling

Although systematic sampling has been recommended to reduce levels of spatial autocorrelation in the data (Smith 1994), this can introduce considerable bias (Green 1979). I randomly sampled plant presence/absence and associated environmental variables from approximately five percent of available sites. The levels of autocorrelation in the data sets were tested using Moran's coefficient. Moran coefficient values of 0 indicate no autocorrelation; values approaching 1 indicate strong positive autocorrelation. Autocorrelation levels were low (Moran's coefficient ranged from 0.0129-0.0277 with a mean of 0.0174).

Logistic regression analysis

I used logistic regression, a type of generalised linear model, to predict the probability of a species occurring as a function of environmental factors (Collett, 1991). Logistic regression is advocated when the response variable is binary (e.g. presence or absence of a species). An appropriate error function for logistic regression is specified by a binomial distribution. The linear logistic model for the dependence of p_i (the success probability of the observation) on the value of K explanatory variables ($x_{1i}, x_{2i}, \ldots, x_{ki}$) is,

$$\log(p_i/(1-p_i)) = \beta_0 + \beta_1 X_{1i} + \beta_{2i} X_{2i} + \cdots + \beta_k X_{ki} \qquad (1)$$

Where p is the probability of occurrence, β_n are constants and X_n area the explanatory varibales. Equation (1) can be rearranged as

$$p_i = \frac{\exp(\beta_0 + \beta_1 X_{1i} + \cdots + \beta_{ki})}{1 + \exp(\beta_0 + \beta_1 X_{1i} + \cdots + \beta_{ki})} \quad (2)$$

(Collett 1991). The probability of a species occurring is a sigmoidal function when the linear predictor is a first order polynomial and a bell-shaped function when the linear predictor is a second order polynomial.

The independent variables were right skewed and therefore square root transformed. The logistic models were fitted in stages using Genstat 5.3 (Genstat 5 Committee 1993). I first investigated the form of the relationship between plant presence and each environmental variable by using cubic splining in the logistic model. Fitting cubic splines, also called generalised additive modelling (Hastie and Tibshirani 1990), is recommended for data exploration because these models allow the data to determine the shape of the response. Generalised additive models are therefore good at detecting skewed or bimodal responses (Yee and Mitchell 1991). Sequentially more complex (models with greater degrees of freedom) generalised additive models were fitted. The simplest model that adequately described the data was selected. A generalised linear model with the same degrees of freedom was fitted. In all cases the generalised additive models did not provide substantially better fits than the generalised linear models. This was assessed by examining the variance explained and the residuals of the fitted models. The best fitting generalised linear model was used in the next phase of model fitting. All marginal effects (effect when a factor is fitted on its own) were significant, i.e. no factors could be excluded from the model at this stage.

The second phase of model fitting aimed to remove all factors from the model that did not significantly improve the model fit. The significance of partial effects of a factor were assessed by checking if there was a significant change in deviance ($p < 0.05$) when the factor was excluded from the full model (model with all factors included). All significance tests were based on the assumption that the change in deviance is distributed as a chi-squared statistic.

Plant diversity impact

Although it is not possible to predict the extinction risk for all species in the study area, it is possible to estimate the level of threat each native species faces. This is done by calculating

the proportion of the range of each species that could be covered by alien plants (as predicted by the logistic regression model). This allows us to estimate how many native species each alien species threatens. The number of species threatened will, however, be strongly correlated with the area the alien species is predicted to invade. This necessitates the construction of a null model to estimate the number of species that would be threatened if the locations of the invaded sites were randomly selected. The null model allows us to estimate the importance of using a spatially explicit approach for quantifying the threat of alien plants. This null model was estimated by randomly selecting the locations of the invaded sites, and then counting the number of species whose ranges would be completely covered by this random distribution of invaded sites. This procedure was repeated 100 times for each of the possible number of sites that could be invaded (1 to 332 1 km^2 sites). This allowed the calculation of the mean number of species threatened for a given area invaded.

RESULTS

Correlations between independent variables

The only strong correlations between the independent variables were between rainfall, altitude and slope (Table 1). Altitude and slope are correlated because higher areas have more rugged topography and hence steeper slopes. Rainfall and altitude are correlated because rainfall on the Cape Peninsula is largely orographic.

Table 1. Matrix of Pearson coefficients of the independent variables

	Flammability	Moisture	Nutrient	Altitude	Slope	Rain	Radiation
Flammability	1.000						
Moisture	-0.183	1.000					
Nutrient	0.316	0.054	1.000				
Altitude	0.014	-0.340	0.074	1.000			
Slope	-0.252	-0.040	-0.348	0.555	1.000		
Rain	-0.130	-0.391	-0.305	0.621	0.454	1.000	
Radiation	0.077	0.169	0.108	-0.186	-0.312	-0.157	1.000

Generalised linear models

The marginal effects of each of the environmental factors were significant, for all alien species, when compared to the corresponding null model that the factor had no influence on the probability of occurrence. The partial effects, however, showed that for *Acacia cyclops* flammability, soil nutrients, altitude slope and rainfall were the most important factors

Table 2. Analysis of deviance table for the final *Acacia cyclops* model

	Deviance	d.f.	
Null model	2637	2665	
Factor	Change in Deviance	Change in d.f.	Significance
Full model	490	10	<0.001
Flammability	26	1	<0.001
Nutrient	18	2	<0.001
Altitude	103	2	<0.001
Slope	61	3	<0.001
Rain	71	2	<0.001

Table 3. Estimates of the final model parameters for *Acacia cyclops*.

Parameter	Estimate	S.E.	*z*-Score
Constant	-22.09	4.75	-4.65
Flammability	-0.2967	0.0609	-4.87
Nutrient	2.093	0.845	2.48
Nutrient^2	-0.563	0.197	-3.14
Altitude	0.2417	0.0528	4.57
Altitude^2	-0.01472	0.00218	-6.77
Slope	-0.523	0.241	-2.17
Slope^2	0.2171	0.0787	2.76
Slope^3	-0.01531	0.00749	-2.04
Rain	1.437	0.346	4.15
Rain^2	-0.02698	0.00619	4.36

Table 4. Analysis of deviance table for the final *Acacia longifolia* model.

	Deviance	d.f.	
Null model	1323	2665	
Factor	Change in Deviance	Change in d.f.	Significance
Full model	214	6	<0.001
Altitude	133	2	<0.001
Slope	38	2	<0.001
Rain	83	2	<0.001

Table 5. Estimates of the final model parameters for *Acacia longifolia*

Parameter	Estimate	S.E.	*z*-Score
Constant	-16.13	5.12	-3.15
Altitude	0.991	0.129	7.71
Altitude^2	-0.03379	0.00432	-7.83
Slope	-0.259	0.229	-1.13
Slope^2	-0.0197	0.0330	-0.60
Rain	0.349	0.351	0.99
Rain^2	-0.00215	0.00589	-0.36

Table 6. Analysis of deviance table for the final *Acacia mearnsii* model.

Parameter	Deviance	d.f.	
null model	1216	2665	
Factor	Change in Deviance	Change in d.f.	Significance
Full model	409	6	<0.001
Nutrient	26	2	<0.001
Altitude	27	2	<0.001
Rain	138	2	<0.001

Table 7. Estimates of the final model parameters for *Acacia mearnsii*.

Parameter	Estimate	S.E.	*z*-Score
Constant	-68.6	10.6	-6.49
Nutrient	4.22	1.04	4.07
Nutrient^2	-1.097	0.243	-4.52
Altitude	0.574	0.138	4.16
Altitude^2	-0.01811	0.00413	-4.38
Rain	3.455	0.702	4.93
Rain^2	-0.0500	0.0112	-4.46

Table 8. Analysis of deviance table for the final *Acacia saligna* model.

	Deviance	d.f.	
Null model	1603	2665	
Factor	**Change in Deviance**	**Change in d.f.**	**Significance**
Full model	341	6	<0.001
Nutrient	13	2	<0.001
Altitude	30	2	<0.001
Slope	20	2	<0.001
Rain	118	2	<0.001

Table 9. Estimates of the final model parameters for *Acacia saligna*.

Parameter	Estimate	S.E.	*z*-Score
Constant	-42.83	5.16	-8.30
Nutrient	2.167	0.815	2.66
Nutrient^2	-0.547	0.180	-3.04
Altitude	0.1002	0.0575	1.74
Altitude^2	-0.00636	0.00199	-3.20
Slope	0.324	0.180	1.80
Slope^2	-0.0116	0.0217	-0.53
Rain	2.428	0.364	6.68
Rain^2	-0.03781	0.00617	-6.13

Table 10. Analysis of deviance table for the final *Pinus pinaster* model.

	Deviance	d.f.	
Null model	2424	2665	
Factor	**Change in Deviance**	**Change in d.f.**	**Significance**
Full model	591	6	<0.001
Nutrient	23	1	<0.001
Altitude	189	3	<0.001
Rain	12	2	<0.001

Table 11. Estimates of the final model parameters for *Pinus pinaster*.

Parameter	Estimate	S.E.	*z*-Score
Constant	-0.901	3.92	-0.23
Nutrient	-0.582	.122	-4.76
Altitude	1.046	.231	4.52
Altitude^2	-0.0525	.0136	-3.87
Altitude^3	0.000970	0.000253	3.83
Rain	-0.489	0.246	-1.99
Rain^2	0.00914	0.00413	2.22

Table 12. Analysis of deviance table for the final *Pinus radiata* model.

	Deviance	d.f.	
Null model	1500	2665	
Factor	**Change in Deviance**	**Change in d.f.**	**Significance**
Full model	466	5	<0.001
Moisture	50	1	<0.001
Altitude	59	2	<0.001
Rain	158	2	<0.001

Table 13. Estimates of the final model parameters for *Pinus radiata*.

Parameter	Estimate	S.E.	*z*-Score
Constant	-56.28	6.72	-8.37
Moisture	-1.080	0.161	-6.70
Altitude	0.567	0.100	5.67
Altitude^2	-0.01747	0.00284	-6.14
Rain	3.183	0.444	7.17
Rain^2	-0.04788	0.00720	-6.65

determining the probability of occurrence (Table 2). Of these factors, it was altitude and rainfall that accounted for most of the variance. The probability of finding *A. cyclops* was predicted to decrease with increasing vegetation flammability and increase with soil fertility. The probability of finding *A. cyclops* was predicted to increase at sites below 400 m in altitude and on flat to gentle sloping sites (<10°). *Acacia cyclops* was more likely at sites with an annual rainfall above 500 mm, most likely at sites above 800 mm, and unlikely at sites above 1100 mm (Table 3). Altitude, rainfall and slope were the factors that significantly influenced *A. longifolia* distribution (Table 4). The chance of finding *A. longifolia* was predicted to increase between 150 and 350 m above sea-level, on moderately steep slopes (5 to 30°). *Acacia longifolia* showed a wide tolerance of rainfall conditions, being predicted to occur from the driest sites on the Peninsula (<400 mm per annum) to sites receiving 1400 mm of annual rainfall (Table 5). Soil nutrients, altitude and rainfall were the factors that most influenced the distribution of *A. mearnsii* (Table 6). *Acacia mearnsii* was more likely to be found on nutrient-rich sites, at lower altitudes away from the coast (200-600 m above sea level), and on sites receiving an annual rainfall between 850-1300 mm (Table 7). Soil nutrients, altitude, slope and rainfall explained most of the variation in the distribution of *A. saligna* (Table 8). The probability of *A. saligna* occurrence increased with soil nutrient levels. *Acacia saligna* showed a preference for sites in the 50 to 550 m altitude range, and with an annual rainfall between 700 and 1300 mm. *Acacia saligna* was predicted to grow on a wide range of slopes, including steep (>40°) slopes (Table 9). Soil nutrients, altitude, and rainfall were the factors that most influenced the distribution of *Pinus pinaster* (Table 10). *Pinus pinaster* was more likely to be found on nutrient-poor soils, but showed a strong preference for sites at higher altitudes and sites that received more than 800 mm of annual rainfall (Table 11). Moisture, altitude and rainfall were the factors that explained most of the variation is the distribution of *P. radiata* (Table 12). *Pinus radiata* showed a preference for sites with moist soils, and in the 200 - 700 m above sea level range. *Pinus radiata* was more likely to occur on sites receiving between 800 mm and 1400 mm of annual rainfall (Table 13).

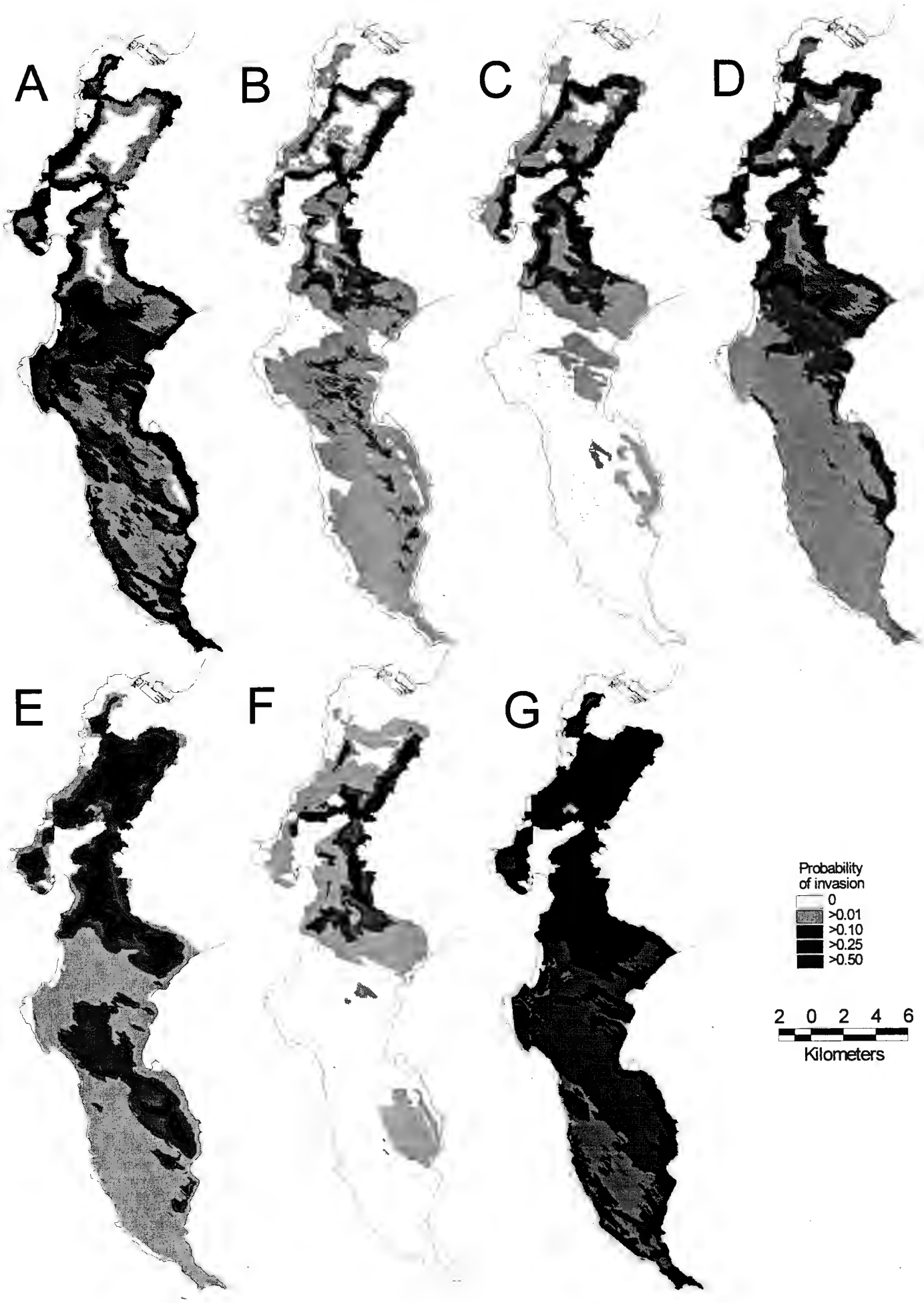

Figure 1. The predicted probability of invasion for *Acacia cyclops* (A), *A. longifolia* (B), *A. mearnsii* (C), *A. saligna* (D), *Pinus pinaster* (E), *P. radiata* (F) and all 6 alien plant species (G) on the Cape Peninsula.

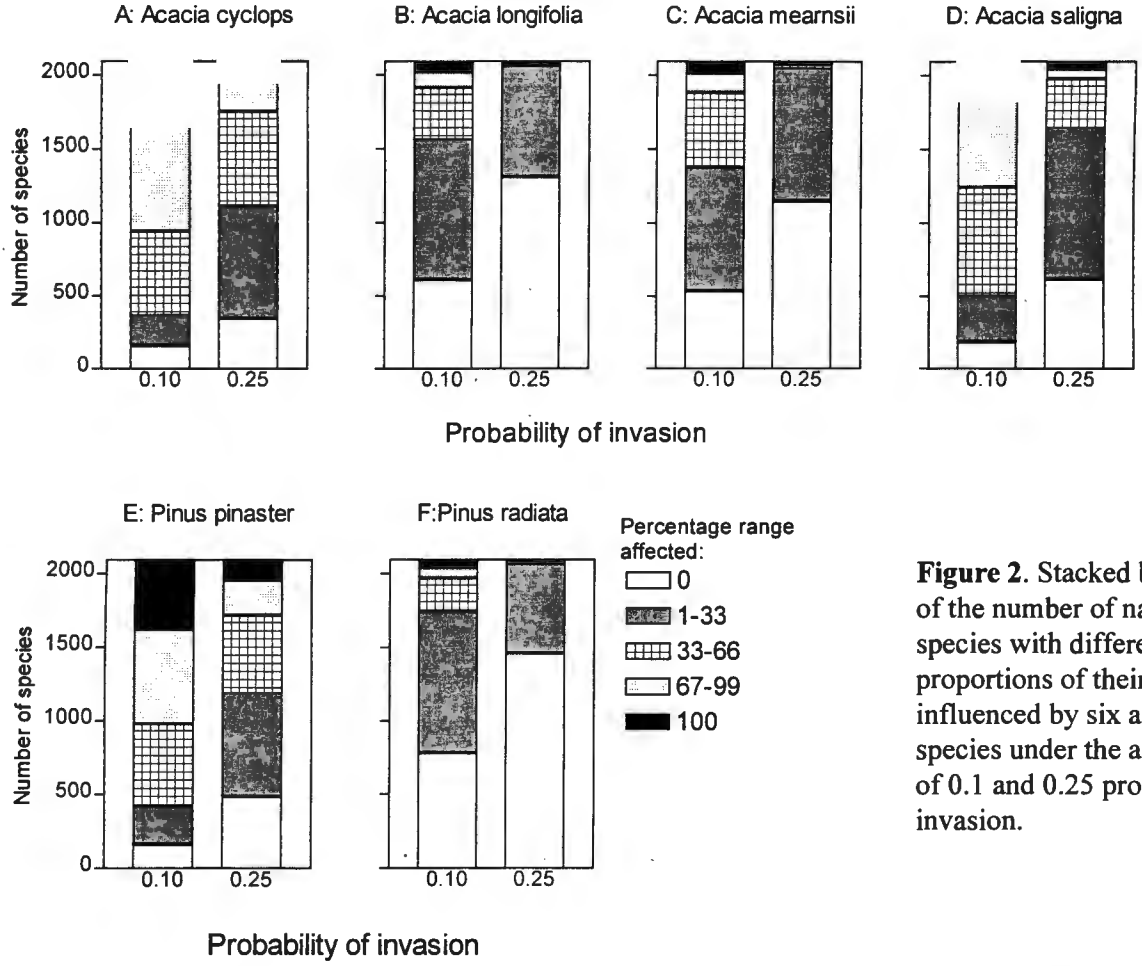

Figure 2. Stacked bar charts of the number of native plant species with different proportions of their ranges influenced by six alien plant species under the assumption of 0.1 and 0.25 probability of invasion.

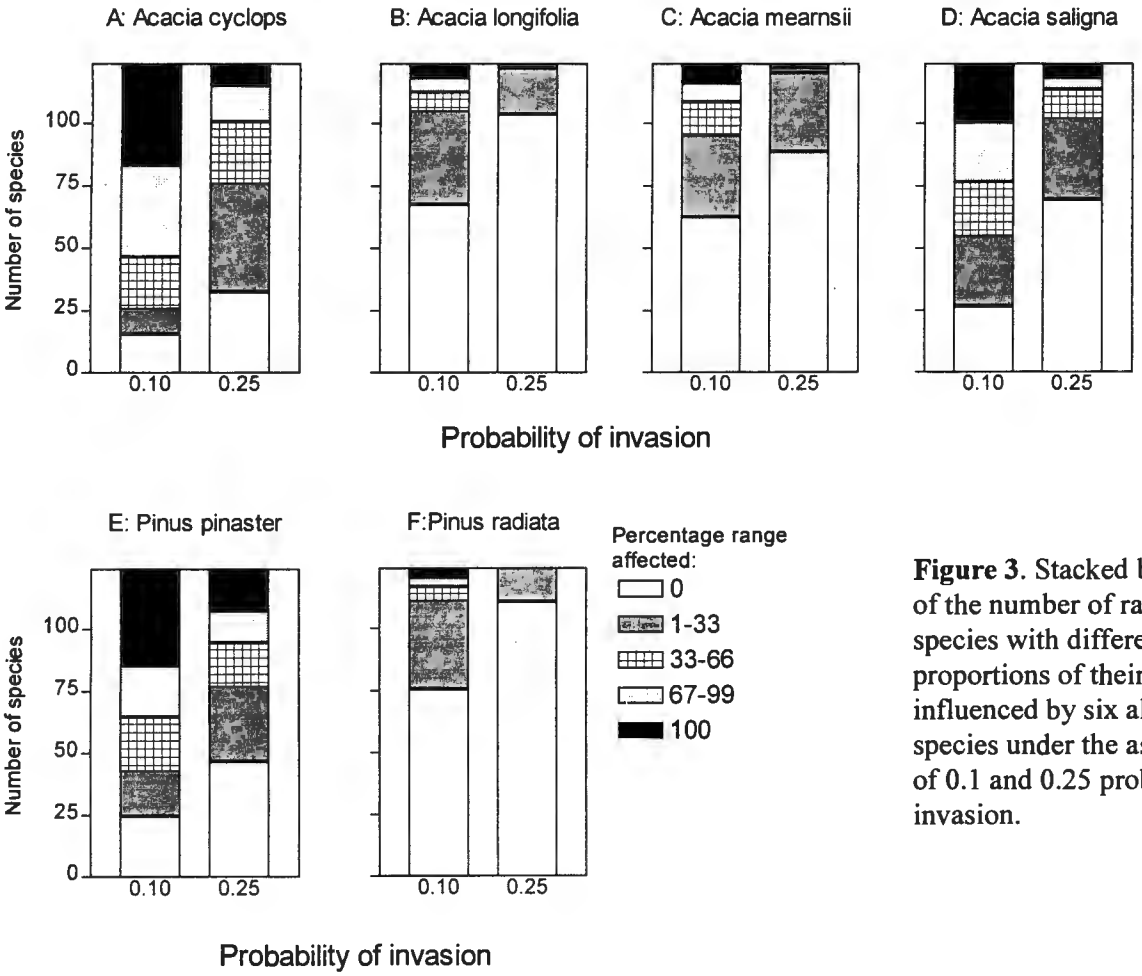

Figure 3. Stacked bar charts of the number of rare plant species with different proportions of their ranges influenced by six alien plant species under the assumption of 0.1 and 0.25 probability of invasion.

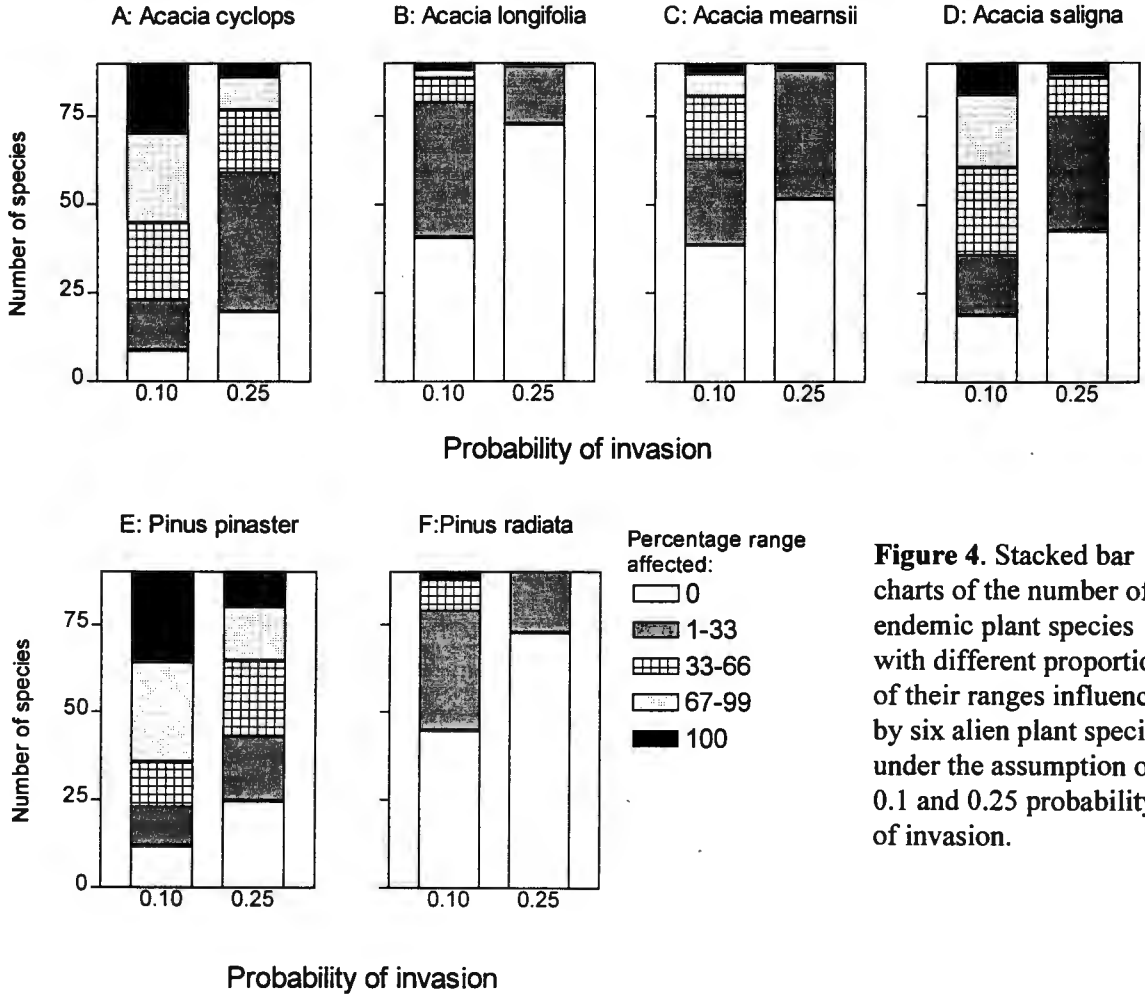

Figure 4. Stacked bar charts of the number of endemic plant species with different proportions of their ranges influenced by six alien plant species under the assumption of 0.1 and 0.25 probability of invasion.

The predictions of the final generalised linear models are presented in Figure 1. *Acacia cyclops* is predicted to cover the greatest area of all species: 64 % of the study area, under the 0.1 probability of invading or 37 % of the study area at the 0.25 probability of invading (Table 14). *Pinus pinaster* and *A. saligna* are also predicted to cover large areas (Table 14). *Pinus radiata*, *A. longifolia* and *A. mearnsii* are predicted to cover much smaller areas (Table 14).

Table 14. The predicted area invaded for six invasive species on the Cape Peninsula (the study area is the 32847 ha of vegetation untransformed by agriculture and urbanisation).

Area invaded	Area (ha) invaded						
	Acacia cyclops	*Acacia longifolia*	*Acacia mearnsii*	*Acacia saligna*	*Pinus pinaster*	*Pinus radiata*	All species
Current	6440	2184	2146	4066	5317	2948	13534
Predicted (p>0.10)	21072	6712	6892	14179	16246	4626	32776
Predicted (p>0.25)	12382	1339	2967	6514	7684	2073	29221

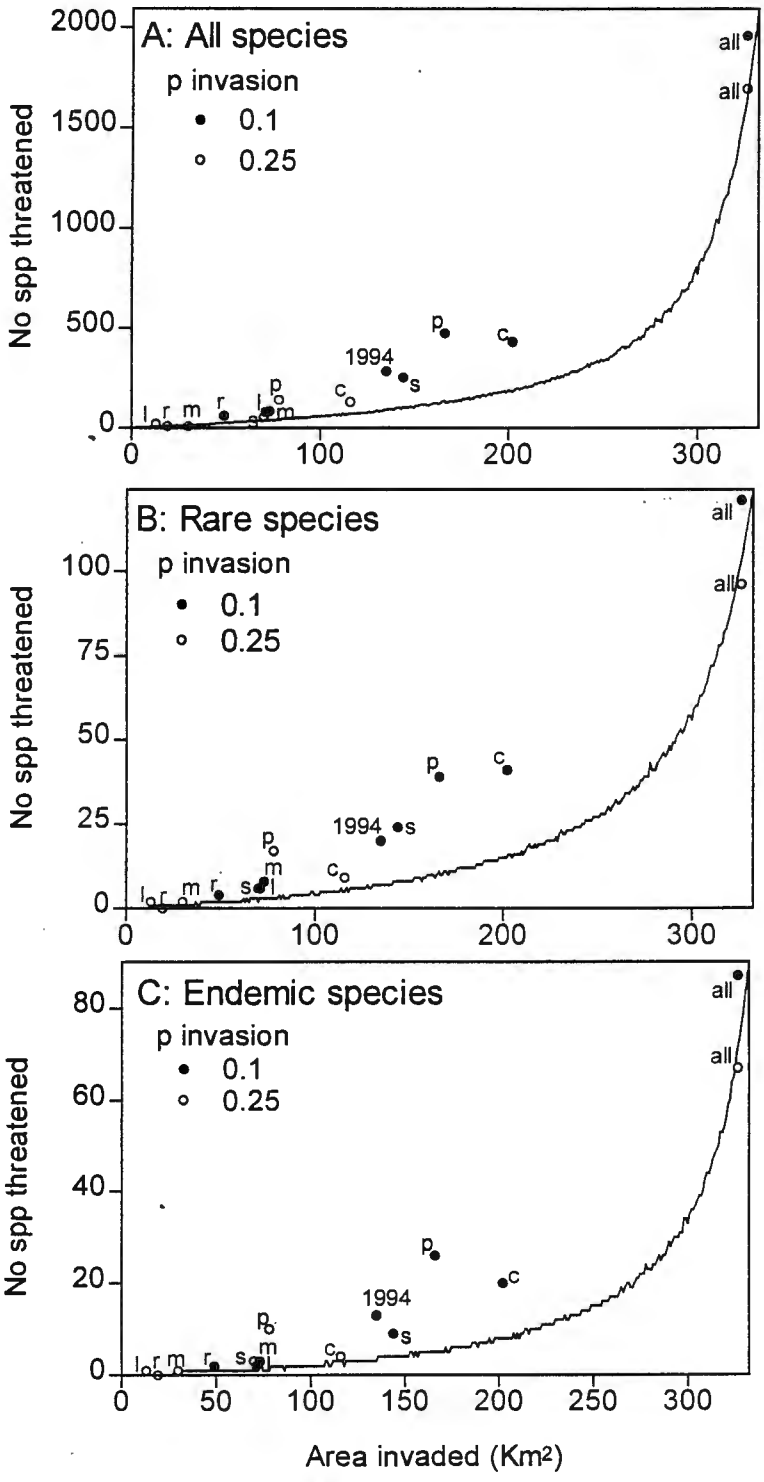

Figure 5. The number of native species that have their entire Cape Peninsula distribution covered by the predicted distribution of each alien species and for all six species. Solid circles are for a 0.1 probability of invasion, open circles are for a 0.25 probability of invasion; the curve is the number of species that would have their entire Cape Peninsula distribution covered if sites were selected randomly; c = *Acacia cyclops*, l = *A. longifolia*, m = *A. mearnsii*, s = *A. saligna*, p = *Pinus pinaster*, r = *P. radiata,* all = all six alien plant species, 1994 = 1994 distribution of all six alien species.

Predicted threats on plant diversity

Pinus pinaster, Acacia cyclops and *A. saligna* have the greatest impact on native, rare and endemic plant species; *A. longifolia, A. mearnsii* and *P. radiata* threatened fewer species (Figures 2-4). This pattern is however strongly influenced by the area each species is predicted to invade (Table 14). Figure 5 shows how much each species' distribution deviates from the null model that assumes that the locations of invaded sites are randomly selected. Most species threaten more native plant species than would be expected if the sites they invaded were randomly selected. The exceptions are for the predicted distributions of *P. radiata* and *A. mearnsii* under the 0.25 probability of invading. These two invasive species threaten the same number or fewer native, rare, and endemic species than the null model predicts (Figure 5). *Pinus pinaster, A. cyclops* and to a lesser degree *A. saligna* threaten substantially more species than would be expected by heir predicted area alone (Figure 5). The threat posed by predicted distribution of all six alien species combined is substantial in comparison to the threat posed by the 1994 distribution of these alien plants (Figure 6). In the 0.10 probability of invasion case 93 % of species, 97 % of rare species and 96 % of endemic species will be threatened. In the more conservative (0.25 probability of invasion) case 81 % of species, 77 % of rare species and 74 % of endemic species will have their entire ranges on the Cape Peninsula covered by alien plants.

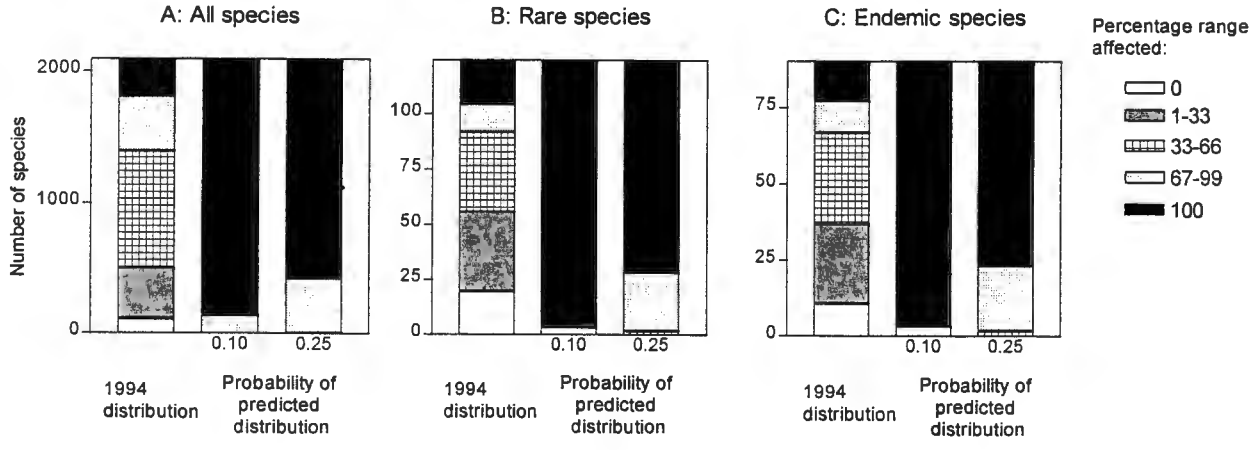

Figure 6. Stacked bar charts of the number of plant species, rare plant species and endemic plant species with different proportions of their ranges affected by the combined distribution of all alien species for 1994 mapped distribution and the predicted distribution under the assumption of 0.1 and 0.25 probability of invasion.

DISCUSSION

Species - environment models

Altitude and annual rainfall are the environmental variables that explained most of the variance in the distribution of six invasive plant species on the Cape Peninsula. Slope, soil moisture, soil nutrient status, vegetation flammability and radiation loads explained less of the variance in species response. The predictions of the logistic regression model show that *Acacia cyclops*, *Pinus pinaster*, and *A. saligna* could cover 38-64, 23-49, and 19-43 % of the Cape Peninsula respectively. *Acacia mearnsii, A. longifolia* and *P. radiata* are predicted to cover 9-21, 4-20, and 6-14 % of the Cape Peninsula (Table 14). The predicted pattern of distribution did not contradict the field observations of experts; although it should be noted that the models are statistical and therefore only relevant to the study site. The models predict that at least one of the six alien species considered in this study will cover between 89 and 99 % of the Cape Peninsula. This latter result is consistent with the results obtained by Richardson et al. (1996) who used a less rigorous modelling approach.

The variance explained by the models was lower (16-34 %) than that typically reported by studies that use generalised linear modelling to describe the environmental preferences of species (e.g. Margules and Stein 1989, Austin et al. 1990). There are a number of potential explanations for this. (1) The model could not describe the data. I used generalised additive models which use spline smoothing to fit complicated response functions in the data exploration stage of this study. Since the generalised additive models did not provide better fits than the generalised linear models I think this source of error is unlikely. (2) The environmental variables in this study do not influence the distribution of alien plants. While I cannot discount this, I believe that the range of environmental variables in the study is adequate when compared to studies that explain greater proportions of the variance (Margules and Stein 1989, Austin et al. 1990). (3) The current distribution of the alien plants is not reflective of their realised niche. This study uses the current distribution to define the realised niche of each alien species. The absence or low abundance of a species at a site may be because it has not arrived or has only recently arrived at that site. It follows that a perfect fit would not be expected under these conditions. This source of error in the model could be discounted if one could assume that each site has historically received propagules of the invading species. For the Cape Peninsula, the long history of widespread planting of alien plant species (all species in this study have been present for more than 100 years, Richardson et al. 1996) suggests that this assumption is not unrealistic. However, this problem is of general importance to similar studies, and more work is

needed to develop techniques to determine when the distribution of alien plants is reflective of their realised niche. (4) The sporadic and uncoordinated clearing of alien plants by management authorities and volunteer groups on the Cape Peninsula (see van Wilgen 1996) introduces another source of error. Clearing also means that absence at a site may not be reflective of the potential range of a species. However, the removal of the Cape of Good Hope Nature Reserve from the analysis, most of which has been kept clear of alien plants, did not improve the fit of the model. Although this suggests that this source of error was not large, the localised and sporadic pattern of clearing of alien plants means that I cannot discount this source of error. (5) An alternative explanation is that the species have wider environmental tolerances than the range of environmental conditions on the Cape Peninsula. This is supported by the observation that all these species also invade other regions with disparate environmental conditions (*Acacia cyclops* invades in California; *A. longifolia* invades in New Zealand and Israel; *A. mearnsii* invades in New Zealand and Hawaii; *A. saligna* invades in California (Cronk and Fuller 1995); while *Pinus pinaster* and *P. radiata* invade many areas (Richardson and Higgins 1998)).

Predicted impacts on plant diversity

The potential impact of the six invasive species on the native plant flora is strongly related to their predicted cover. However most species will pose a greater threat to plant diversity than their area alone suggests. This is because the areas of high plant diversity on the Cape Peninsula (see Trinder-Smith 1996b) are also the sites where invasive species are predicted to invade. This result agrees with the theory that species-rich sites are more easily invaded (Robinson et al.1995). However Tilman (1997) has presented experimental evidence that species-rich communities resist invasion. Rejmanek (1996) has hypothesised that functional diversity and not its sometime correlate, species diversity, determines openness to invasion. This study suggests that more explicit testing of the relationships between functional diversity, species diversity and openness to invasion is needed.

The spatially-implicit null model of the threat posed by alien plants underestimates the number of native species threatened by 350 (380%), the number of rare species by 29 (390%), and the number of endemic species by 21 (520%) in the case of *Pinus pinaster*. The study therefore shows that *P. pinaster* poses the greatest threat to the native plant diversity of the Cape Peninsula despite the fact that *Acacia cyclops* is predicted to invade the greatest area. Because *P. pinaster* is easy to clear and has a longer time to reproductive maturity than the *Acacia* species, managers regard clearing *P. pinaster* as a low priority. However, its threat to plant

diversity suggests that *P. pinaster* should receive a high priority. This study shows that a spatially-explicit model of threats to plant diversity should be used to define strategies for mitigating threats.

CONCLUSION

The threat posed by alien plants to the plant biodiversity of the Cape Peninsula is severe. The results presented here quantify the magnitude of the threat. More importantly, these results can be used to prioritise which sites and which alien species require urgent attention. This study shows the value of adopting a spatially explicit approach for quantifying the threat to biodiversity and that errors associated with spatially-implicit models could be substantial. The maps of where the species are predicted to invade will also be useful when integrated with dynamic spatially explicit simulation models of alien plant spread (e.g. Chapters 3, 4 and 8). This would allow the integration of information on the environmental tolerances of invasive species with information on the spatial demography of invasions. These models will allow the assessment of the rates of invasion and native plant threat under different policy and management scenarios (Chapter 8).

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A DYNAMIC SPATIAL MODEL FOR THE MANAGEMENT OF ALIEN PLANT INVASIONS AT THE LANDSCAPE EXTENT

Abstract. Biological invasions are widespread phenomena that threaten the integrity and functioning of natural ecosystems. I developed a model that is designed to be a decision making tool for planning and managing alien plant control operations. Most decision tools adopt a static approach; in this application I integrate a dynamic simulation model of alien plant spread with decision making tools commonly used for reserve design. The model is a landscape-scale implementation of a fine-grained individual-based simulation model. I first describe the scaling up of this fine-scaled model into a landscape extent model. I show that the scaling up processes do not introduce unreasonable artefacts into the behaviour of the model. I then explore a range of clearing strategies and funding schedules for clearing alien plants. These clearing scenarios are evaluated in terms of the cost of the clearing operation, the time it takes to eradicate the plants, and the impact the plants have on three components of native plant diversity. Clearing strategies that prioritise low-density sites dominated by juvenile alien plants proved to be the most cost-effective. Strategies that used information on the distribution of plant diversity were not much more expensive than the most cost effective strategy and they substantially reduced the threat to three components of native plant diversity. Delaying the initiation of clearing operations had the strongest effect on both the eventual costs of the clearing operation and the threat to native plant diversity. I conclude that the integration of dynamic modelling with decision-making tools, as illustrated here, will be useful for the management of biodiversity under global change.

Keywords: Biological invasions, spatial modelling, scaling up, decision making, biodiversity, clearing strategy.

INTRODUCTION

The impacts of biological invasions are so widespread and significant that biological invasions are a recognised component of global change (Vitousek at al. 1996). Plant invasions have been shown to impact on both human-altered and pristine systems in a number of ways. The invasion of American rangelands by *Bromus tectorum* has increased the frequency and intensity of fires, thereby transforming woodlands to grasslands (Whisesant 1990). Similarly,

the invasion of alien grasses into Californian chaparral has resulted in more frequent and intense fires, which, in turn, have altered species composition (Zedler et al. 1983). The invasion of the nitrogen-fixing shrub, *Myrica faya*, on volcanic surfaces in Hawaii dramatically altered patterns of nutrient cycling (Vitousek and Walker 1989). The alien tree *Melaleuca quinquenervia* raises soil elevations and thereby influences the hydraulics of Florida wetlands (Schmitz et al. 1997). Invasions of *Acacia* and *Pinus* spp. into the fynbos of South Africa have dramatically reduced the water yield of catchments (Le Maitre et al. 1995). *Mimosa pigra* invasion into northern Australia is predicted to lead to the collapse of plant and animal populations (Braithwaite et al. 1989), while the invasion of a variety of alien plants into South African fynbos threatens many species in a flora characterised by exceptional levels of endemism (Musil 1993). The economic cost of invasions can be considerable: the cost of the Zebra Mussel and Golden Snail invasions run into millions of dollars annually (Vitousek et al. 1996). These costs, which influence market goods and services, are relatively easy to estimate. However many invasions influence ecosystem services, the value of which falls outside conventional valuation schemes. A recent attempt to quantify how plant invasions reduce the value of the services provided by natural ecosystems (Higgins et al. 1997) suggests that the costs of biological invasions are more considerable and far reaching than is presently acknowledged.

The best way to mitigate the impacts of plant invasions is to prevent the introduction of high-risk taxa. A number of screening schemes that facilitate the identification of high-risk taxa have been developed (e.g. Tucker and Richardson 1995, Rejmanek and Richardson 1996, Reichard and Hamilton 1997). However, in many cases it is too late for preventative action. In this chapter I, therefore, concentrate on developing strategies for controlling plant invasions. The development of an effective strategy for alien plant management requires an ability to predict the rates and patterns of invasive plant spread. Predicting invasion rates and patterns is itself the first step in quantifying the impacts of an invasion. Knowledge of the rate and pattern of invasion and of the potential impacts of an invasion is necessary for defining a control strategy that is both cost-effective and mitigates the cumulative impact of the invasion.

Despite the many management models being developed and significant developments in theoretical models of spread (Andow et al. 1990, Hengeveld 1994, Shigesada et al. 1995, Clark 1998, Chapters 3 and 5) few models have been applied to alien control problems (Chapter 2). Moody and Mack's (1988) contribution remains a notable exception. Their

conclusion that the most cost-effective strategy is to clear small isolated stands first remains the key guiding principle of many alien-clearing operations. However, I caution that few generalisations have emerged from almost two decades of research into biological invasions (Lodge 1993). This has been attributed to the importance of interactions between plants, environment and disturbance in invasions (Chapter 4). This means that models capable of simulating the interactions between plant and environment are essential for predicting invasions. The importance of these interactions and the critical importance of invasion rates in defining a management strategy mean that static rule-based decision support systems (e.g. Ralls and Starfield 1995) are unlikely to be useful. Moreover, because the distribution of alien plant threat and system vulnerability is unlikely to be uniform, a spatially explicit approach is necessary (Chapter 7).

I have developed and validated a spatially explicit, individual-based (SEIBS) simulation model that predicts rates and patterns of alien plant spread (Chapters 3, 4, 5 and 6). Since the SEIBS model is individual-based, it has only been applied to a relatively narrow spatial extent. To be relevant at the scale at which managers make decisions, the SEIBS model must be scaled up to the landscape extent. I will call this scaled up model the spatially explicit, landscape-extent simulation (SELES) model. Because ecologists are constantly required to integrate information across scales, the scaling up of models is a central issue in landscape ecology (Turner et al. 1989, King 1991, Levin 1992). Scaling up usually involves aggregating the behaviour of the underlying model and integrating constraints and processes that become important at the larger spatial extent. Aggregation is usually done to keep the model computationally tractable: for example, a scaled up version of the SEIBS model will have to increase the model's grain to keep it computationally tractable. One possible approach to the aggregation problem is to link a Markov state and transition approach with the spatially explicit simulation paradigm of cellular automata (e.g. Acevedo et al. 1995, Li and Reynolds 1997). Another approach is to aggregate the behaviour of individual plants into patches (e.g. Chapter 3). The state and transition approach is preferable when the processes in the fine scale model are continuous, complex, non-linear, and/or computationally demanding (Rastetter et al. 1992). It follows that the state and transition approach is recommended for scaling up a JABOWA-FORET model (e.g. Acevedo et al. 1995). Since the SEIBS model concentrates on simulating simple demographic processes that occur discretely, aggregating the behaviour of an individual into a patch is possible. Environmental heterogeneity usually increases with increasing extent and this needs to be included in a scaled up model. For example altitudinal gradients can often be ignored at the 20 km^2 extent, but not at the 500

km^2 extent. Which landscape extent processes and constraints are integrated into the model is strongly dependent on the system and scale. Existing methods for simulating these landscape-extent processes usually exist. For example, if fire is an important landscape-extent process, an existing fire spread model can be integrated into the model.

The aims of this chapter are to (1) develop a scaled up, landscape extent, version of an existing spatially explicit individual-based simulation; (2) use the spatially explicit, landscape extent simulation (SELES) model to explore the potential impact of alien plants on a native ecosystem; (3) use the SELES model to define clearing strategies that optimise cost effectiveness and minimise the threat to native ecosystems. To achieve this I use the case study of the invasion of *Pinus pinaster* and *Acacia cyclops* into the fynbos-dominated Cape Peninsula, South Africa.

METHODS

The case study

The Cape Peninsula

The dominant vegetation of the Cape Peninsula is fynbos, a mediterranean-type shrubland (see Cowling et al. 1996 for a detailed description of the Cape Peninsula). Fynbos, the dominant vegetation of the Cape Floristic Region (90 000 km^2), is characterised by anomalously high levels of plant diversity and endemism (Cowling et al. 1992) and the Cape Peninsula is itself a centre of diversity within the Fynbos biome (Simmons and Cowling 1996). The Cape Peninsula (471 km^2) is home to 2285 plant species, 90 of which are endemic (Trinder-Smith et al. 1996a).

Native plant diversity is the main component of biodiversity on the Cape Peninsula (Cowling et al. 1996). The major threats to plant diversity are urbanisation and alien plant invasions (Richardson et al. 1996). Agriculture and urbanisation have transformed about 37 % of the original area of natural vegetation. Of the remaining area, 10.7 % is densely invaded and 32.9 % is lightly invaded (Richardson et al. 1996). The most abundant alien species are *Acacia cyclops*, *A. saligna*, *Pinus pinaster* and *P. radiata*. A logistic regression analysis of the potential ranges of alien species on the Cape Peninsula predicted that *A. cyclops* and *P. pinaster* would cover the greatest area (Chapter 7). Chapter 7 predicted that alien plants

would cover at least 89 % of undeveloped land on the Cape Peninsula. The recent proclamation of most of the undeveloped parts of the Cape Peninsula as a national park and the limited potential for future urbanisation (Richardson et al. 1996) means that alien plants pose the greatest threat to the remaining plant diversity of the Cape Peninsula. At present 141 plant species on the Cape Peninsula are classified as Red Data Book species (Trinder-Smith et al. 1996b).

Spatial data

The remaining undeveloped land (32847 ha) on the Cape Peninsula defined the study area. This study used digital maps of the natural vegetation types (Cowling et al. 1996), alien plant distributions (Richardson et al. 1996), roads (Surveyor General), potential alien plant distribution (Chapter 7), and the priority species score (Trinder-Smith et al. 1996b). The priority species score is a cumulative index. Each of the 167 endemic and threatened plant species on the Cape Peninsula is given a score based on its Red Data Book status; the cumulative score for each 1km^2 site (resolution of the species data) is the priority species score (Trinder-Smith et al. 1996b). The maps of potential alien plant distribution are based on a logistic regression model, and therefore include the composite effect of several environmental variables (see Chapter 7).

Spatially explicit landscape extent simulation model

The philosophy behind SELES was to develop a user-friendly model that could be used by a manager or policy maker. The emphasis was therefore on developing simple and efficient algorithms. SELES is a grid-based simulation model that is run on an annual time-step. The grain of the model can be varied; for the Cape Peninsula I use a 200x200 m grain. The model consists of several interacting components: fire spread, plant spread, alien plant clearing and impact evaluation. Each is discussed in the sections that follow.

Fire spread

Fire spread is modelled as a stochastic process, where the probability of fire spread is a function of the fuel load (e.g. Turner and Romme 1994). I used the map of the vegetation types of the Cape Peninsula and the predicted age-specific flammability of these different vegetation types (Le Maitre and Marais 1995) to estimate the probability of fire spread. The

road network of the Cape Peninsula was used to create a series of firebreaks. The user controls the number of ignitions per year; the location of ignition events is randomly selected. An ignition translates into fire spread if the fuel at the site is flammable. The prevailing winds during the summer fire season on the Cape Peninsula blow from the south-east. This has important consequences for the fire return interval; sites near the southern tip of the peninsula, in particular, are seldom burnt (Privett 1998). For this reason the model only allows fires to spread into cells to the north, east and west of a burning cells; spread occurs if the fuel in these adjacent cells are flammable. The model does no simulate fire-spotting. In order to evaluate if the fire spread model yielded reasonable behaviour I ran the fire component of the SELES model for a thousand years and recorded the fire return interval of each site.

Alien plant spread

The plant spread component is an aggregated version of the SEIBS model. The SEIBS model and its assumptions have been described in detail elsewhere (Chapters 3,4,5,6). The most important change is that the SELES model simulates the dynamics of monospecific stands of alien plants rather than individual plants. The stand size is equal to the model's cell size and each stand can only be occupied by a single species. SELES keeps track of the identity of the alien species in each stand, the age of the stand, the density of alien plants in the stand, and the spatial distribution of each alien species' recruitment potential.

Invasion of alien trees and shrubs into fynbos is driven by fire. The fire-return interval for fynbos ranges from 4 to 40 years, although fire frequencies between 8 and 25 years are more typical (van Wilgen 1987). Almost all recruitment occurs after fire and fires cause heavy mortality of both native and alien plants (Richardson et al. 1992). An empirical technique was used to estimate the spatial distribution of recruitment potential. The potential number of recruits (*R*) contributed by an individual plant to a site *m* meters away is,

$$R = \left[STR\left(\frac{dbh}{10}\right)^2 \right] \frac{1}{n} \left[e^{-dm^3} \right] \quad (1)$$

where *STR* is the standard total recruitment and *dbh* is diameter at breast height (Ribbens et al. 1994). I use empirical estimates of *STR* and *dbh* as a function of age for both *Acacia cyclops* and *Pinus pinaster* (Table 1). The recruitment potential of a stand is the product of

the individual recruitment potential and the stand density. The model assumes that recruitment can only occur after a fire or in sites disturbed by alien clearing (see below).

A dispersal function is used to distribute the recruitment potential. The dispersal function is based on a mixture of Weibull distributions (Chapter 5). A mixture of Weibull distributions can be described as,

$$g(x) = p_1 b_1 c_1 (b_1 x)^{c_1 - 1} \exp\left\{-(b_1 x)^{c_1}\right\} + \ldots + p_k b_k c_k (b_k x)^{c_k - 1} \exp\left\{-(b_k x)^{c_k}\right\} \quad (2)$$

where p_i is the proportion, b_i is the scale parameter, and c_i is the scale parameter of the i^{th} component of the mixture. Simulating a mixture distribution allows us to simulate both local and long-distance dispersal (Chapter 5). It was assumed that dispersal was not directed. To improve the computational efficiency, recruits dispersed by the first two components of the mixture model (local dispersal) were collectively dispersed to the parent stand's neighbourhood. The size of this neighbourhood was large enough (4 km^2) to include the locally dispersed recruits. The long-distance recruits (p_3 of the recruits produced by a stand) were dispersed individually using a random direction (0-360°) and a Weibull random number with parameters b_3 and c_3. Modelling dispersal in this way ensures that the model simulates both the mass action of local dispersal and the stochastic nature of long distance dispersal. Parameters for the dispersal functions are listed in Table 1.

The probability of fire-survival (P_s) can be described by a sigmoidal function that can be estimated from data on size-specific mortality. For *Pinus pinaster,* this function is,

$$P_s = 0.0441 + \frac{(0.0819 - 0.0441)}{1 + \exp\left(\frac{10.784 - dbh}{1.060}\right)} \quad (3)$$

(Chapter 6). No relationship between size and mortality probability exists for *Acacia cyclops* and a constant probability (0.0168, Chapter 6) of fire survival was assumed. Since *A. cyclops* and *P. pinaster* do not resprout, this relationship can be used to describe the thinning of stands of alien plants by fire. The model was not sensitive to mortality (Chapter 3) and it is held constant for all simulations. The recruitment and mortality functions need to be linked to a growth function. Following Chapter 6, stem diameter (*dbh*) is estimated as a function of age (*a*),

$$dbh = m\left(1 - e^{-ra}\right) \quad (4)$$

where m is the maximum diameter and r is the growth rate. The parameters are m = 41.4 and r = 0.0669 for *P. pinaster* and m = 20.4 and r = 0.093 for *A. cyclops* (Chapter 6).

The spread of alien plants is constrained by their environmental preferences. Not all sites on the Cape Peninsula are suitable for all species. I use a statistical model of the environmental preference of each species to define their potential ranges. The estimation of these logistic regression models is described in Chapter 7. For a species to recruit at a site, it must first have recruitment potential at that site; the site must have been disturbed by fire or alien clearing operations; and the site must have suitable growing conditions (as defined by the logistic regression model). Since the model assumes single species stands rules for site competition need to be defined. If both species have recruitment potential at a site then the species that is in possession of the site will retain the site. A species can only be displaced by another species if that species has a higher recruitment potential at that site and a higher environmental preference for that site. These competition rules essentially simulate a weighted lottery for site dominance.

To evaluate whether the spread routines of SELES produced reasonable behaviour I compared the spread rates predicted by SELES to those predicted by SEIBS. I used factorial combinations of the fire-frequency, recruitment, and dispersal functions (Table 1) for both *Pinus pinaster* and *Acacia cyclops* for these verification runs.

Table 1. Lower, medium and rapid parameter levels used for the scaling and scenario analyses for *Pinus pinaster* and *Acacia cyclops* (f = fire return interval#; STR = standard total recruitment*; p_i, b_i, c_i = parameters of a mixture of Weibull distributions used to describe dispersal+). Parameter estimates are from Chapter 6.

Parameter	*Pinus Pinaster*			*Acacia cyclops*		
	low	medium	rapid	low	medium	rapid
F	10	15	20	10	15	20
STR	3	15	27	3	40	80
p_1	0.912	0.953	0.953	1	1	0.001
p_2	0.088	0.047	0.046	0	0	0.999
p_3	0	0	0.001	0	0	0
b_1	0.166	0.0625	0.0625	0.333	0.04	0.04
b_2	0.0238	0.0156	0.0156	-	-	0.002
b_3	-	-	0.0001	-	-	-
c_1	1.778	1.983	1.983	1	1	1
c_2	1	1	1	-	-	1
c_3	-	-	1	-	-	-

#only used for the scaling runs, *equation 1, +equation 2.

Table 2. Cost of clearing alien plant species in fynbos for stands of different density and age (R*/ha, Versfeld et al. 1997).

	Light (<25%)	Medium (25-75%)	Dense (>75%)
Mature stands	585	1112	3844
Immature stands	449	812	1218

*R1=RUS$4.8

Alien plant clearing

This component of the model simulates the removal of alien plants from sites, subject to the availability of funds. The annual budget for clearing and the lag in initiating clearing are user-defined parameters. I used management records form actual clearing operations in fynbos to estimate the costs of clearing (Table 2, Versfeld et al. 1997). These data distinguish between the cost of clearing mature stands and juvenile stands and the cost of clearing of light, medium, and dense stands. Light stands are defined as those with < 25 %, medium stands as 25-75 %, and dense stands as > 75 % alien plant cover. The clearing costs are similar for both species (Versfeld et al. 1997) and I ignore these differences here. For the Cape Peninsula clearing rate is limited by the availability of funds and not clearing capacity.

Many different strategies of clearing are possible, and I consider only six strategies here. Developing a clearing strategy involves ranking sites according to some criterion, and then clearing sites sequentially according to their ranking. The first strategy ranks dense sites highest, the second strategy ranks sparse stands highest. Because stands of young plants are reproductively immature and cheaper to clear, some managers prioritise these stands for clearing. Strategies three and four simulate this strategy. The third strategy ranks immature stands highest and mature stands lowest; within these divisions stands are ranked by density. The forth strategy also ranks immature stands highest and mature stands lowest; however within these divisions stands are ranked by their sparseness. The fifth and sixth strategies aim to minimise the threat to plant diversity. These two strategies use the *irreplaceability* and *vulnerability* concepts of reserve design paradigms to define the *conservation priority* of sites (Pressey et al. 1996) and thereby establish priorities for clearing. Irreplaceability is a measure of the likelihood that an area will be needed to achieve a conservation goal; vulnerability is a measure of the relative vulnerability of the biodiversity of an area to the threatening processes. Thus, irreplaceability is a measure of conservation value whereas conservation priority is the value of an area combined with some assessment of it vulnerability and hence the urgency with which it should be conserved (Pressey 1997). The priority species score, which is based on the number and type of Red Data Book plant species at a site (see *spatial*

data above), defines irreplaceability. The density of alien plants defines vulnerability. Strategy five clears dense stands that have a high species priority score (i.e. vulnerable and irreplaceable sites). This strategy uses an equal weighting of the strategy 3 score (juvenile and dense stands) and the priority species score to rank sites. The sixth strategy uses the strategy 4 score (juvenile and sparse stands) equally weighted with the priority species score to rank the sites.

The clearing algorithm uses the ranking to sequentially clear sites until the clearing budget is exhausted. The disturbance associated with clearing dense stands often creates opportunities for the subsequent establishment of alien plants. Moreover, clearing dense stands often involves the burning of the cleared material. This is simulated in the model by burning recently cleared adult stands that have a cover greater than 50%.

Impact evaluation

The impact of alien plants on native plants is well documented for fynbos. Musil (1993) showed that fynbos plants in invaded sites had a 40-80 % higher chance of recruitment failure, and hence local extinction, than in uninvaded sites. It follows that native plants in invaded sites face a high probability of extinction within our planning horizon. Richardson et al. (1989) provided evidence for local extinction by showing that invaded sites in many parts of the fynbos biome have less than half the plant species richness of matched uninvaded sites. In a survey of seedling emergence from seed banks on the Cape Peninsula, Holmes and Cowling (1997) provide similar evidence: invaded sites had 60-86 % lower plant species richness. This model is obviously not detailed enough to predict native plant extinction events. Some functional groups are sensitive to the presence of alien plants and others are remarkably resilient (Holmes and Cowling 1997). Two observations guided the development of a cumulative index of threat. First, a species that has some critical proportion of its range covered by alien plants is under greater threat. Second, the greater the number of years that this critical threshold is exceeded, the greater the threat. The cumulative threat index is calculated by counting, for every simulation year, the number of species that have a critical proportion (>0.75) of their range covered by native plants. A cumulative threat index is calculated for all native, rare and threatened, and endemic plant species (Trinder-Smith et al. 1996b).

Scenario definition

The scenarios are designed to explore the effects of different funding schedules and clearing strategies on the cost effectiveness of a clearing operation and its ability to mitigate the negative impacts of alien plants on native plant diversity. These scenarios are evaluated in the context of our uncertainty of the potential spread rates of alien plant species. For this reason all scenarios are run for a low, medium, and rapid parameterisation of the spread model (Table 1). All simulations are run for 50 years, as this is the extreme planning horizon of even the most dedicated conservation body. Although this may seem like a long time, it is likely to include only two to five fire cycles.

I first run a series of scenarios that identify the most cost-effective clearing strategy that minimises the threat to native plant species. Annual clearing budgets of R0 to R3.6 million are explored for each of the six clearing strategies (see *Alien plant clearing*). This range of funding includes the amount currently spent of clearing and the amounts that a proposed Global Environmental Facility project could deliver (Anon. 1998). For each of these scenarios I record the years taken to remove alien plants from the Cape Peninsula, the total amount spent and the cumulative threat indices for native, rare and threatened, and endemic plant species.

The second series of scenarios examines the details of the funding schedule in more detail. The best clearing strategy is used for all these scenario runs. Annual clearing budgets of R0 to R3.6 million and lags in initiating clearing of 0, 5, and 10 years are explored. For these scenarios I record the years taken to remove alien plants from the Cape Peninsula, the total amount spent and the cumulative threat indices for native, rare and threatened, and endemic plant species. The incentive for a funding agency to delay clearing lies in the discounted cost of that delay. Evaluating whether it makes sense to delay depends on how rapidly the costs escalate due to delaying, as well as the discount rate. Low present values of the cost of delaying clearing would imply that there is a strong incentive to delay. To investigate this I calculate the present value of the cost of delaying for different discount rates and different annual clearing budgets. Because there is a debate surrounding selecting an appropriate discount rate to use in environmental planning (Pearce and Turner 1990, Perman et al. 1996), I explore a range of possible rates.

RESULTS

Model behaviour

The rate of spread predictions made by the SEIBS and SELES models are similar over a range of parameterisations (Figure 1). These runs exclude the effects of environmental heterogeneity and therefore only demonstrate that scaling artefacts are not influencing the model's behaviour. The behaviour of the fire-spread model can be summarised by observing the fire return intervals predicted by the model (Figure 2). This pattern did not contradict the expectations of experts or existing data on the fire return intervals for the southern Cape Peninsula (Privett 1998). The fire model simulates the effect of the Peninsula: the more southern sites have lower fire-return intervals. It also simulates the low fire return intervals characteristic of the forest, dune fynbos, and thicket vegetation types and the high fire return intervals of the fine-fuelled restiod vegetation of the central-southern Peninsula. Figure 3 shows how the area invaded by *Acacia cyclops* and *Pinus pinaster* increases over time on the Cape Peninsula and the corresponding increase in the cumulative threat index to native plant species. The rate of increase can be estimated by assuming that the invasion follows a logistic growth model (Chapter 2). The estimated spread rates were 0.026 (R^2=0. 950) for the low scenario, 0.034 (R^2= 0.961) for the medium scenario and 0.057 (R^2=0. 997) for the high spread scenario. Depending of the parameterisation (low, medium, or rapid) the SELES model predicts that in 50 years the two species will occupy 75, 85, or 95 % of suitable habitat on the Cape Peninsula.

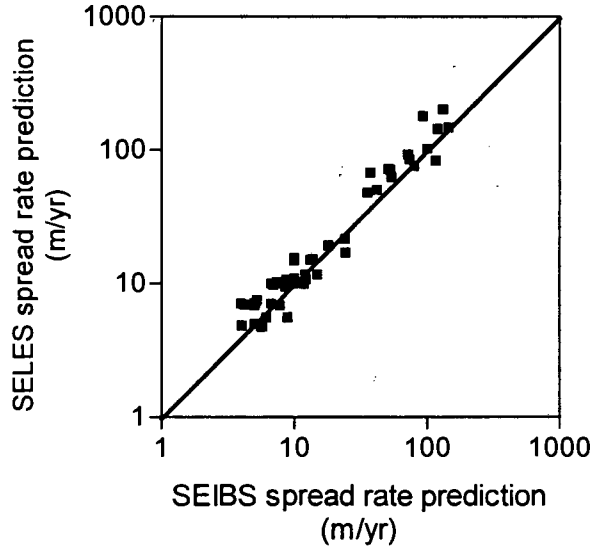

Figure 1. Comparison of the spread rate predictions of the fine-grained (10x10 m) SEIBS and coarse-grained (200x200 m) SELES models for a range of parameterisations for *Acacia cyclops* and *Pinus pinaster*. The parameterisations are defined in Table 1.

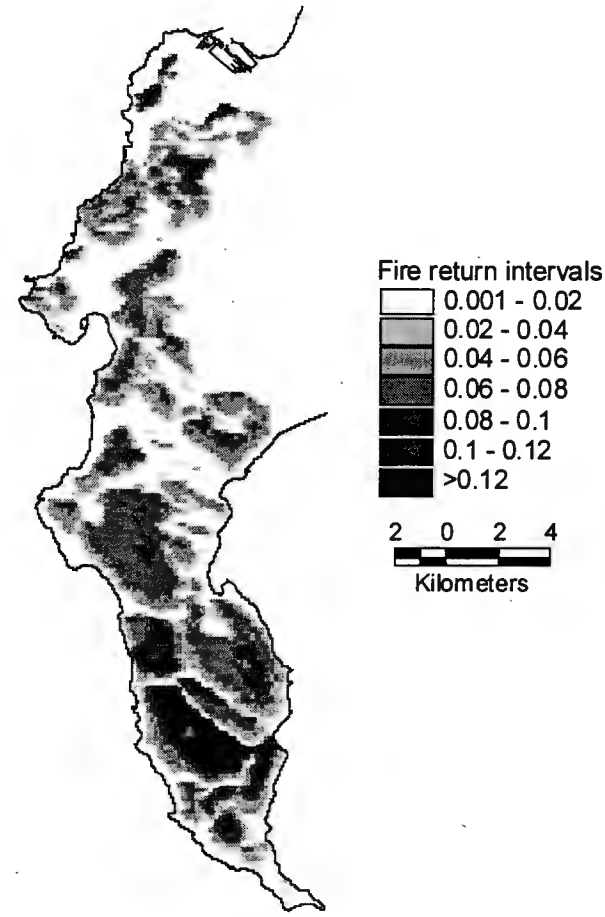

Figure 2. The predicted fire return intervals for the Cape Peninsula. This prediction was made by running the fire sub-model for a thousand years.

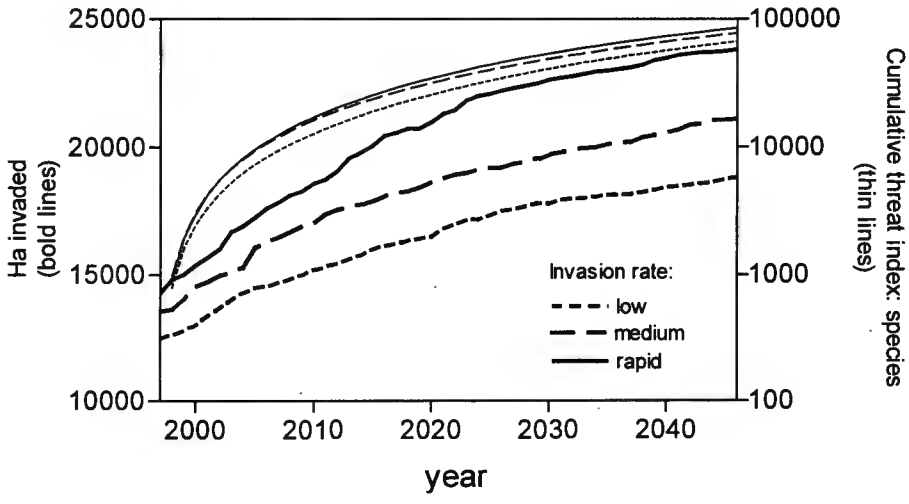

Figure 3. The increase in area invaded by *Acacia cyclops* and *Pinus pinaster* on the Cape Peninsula and the threat this causes to native plant species.

Clearing strategies

Figure 4 shows how the alien clearing strategy and alien clearing budget influences the five response variables for three rates of alien plant spread. The total amount spent on the clearing operation shows that (1) it will cost at least R25 million to clear alien plants from the Cape Peninsula. However this cost could be as high as R55 million depending on how rapidly alien plants spread and the clearing strategies one adopts. The invasion rate strongly influences the cost of clearing. The scenarios that assumed a low invasion rate would cost at most 37 million; whereas the cost of clearing could be as high as R55 million for the medium and rapid spread rates. For low spread rates and high annual clearing budgets the clearing strategy has less influence on the cost of the clearing operation, since the clearing rate is high relative to the rate of spread. At higher spread rates and lower annual budgets using an inefficient strategy can be expensive since the difference between spread rate and clearing capacity magnifies any inefficiency. The scenarios suggest that strategies that prioritise juvenile stands (strategies 3 and 4) are more cost effective than those that do not (strategies 1 and 2); and that clearing sparse stands first (strategies 2 and 4) is more cost effective than clearing dense stands first (strategies 1 and 3). The shape of relationship between total spent on a clearing program and the annual clearing budget indicate that for a given spread rate a critical annual budget exists, above which increases in annual budgets do not reduce the total cost of the clearing operation. However, below this critical budget increasing the annual budget has a large impact on the total cost of the clearing operation. The number of years it takes to clear all alien plants from the Cape Peninsula ranges from 10 to more than 50 years depending on the annual clearing budget. The clearing strategy does not influence the time it takes to clear as much as the annual clearing budget does, although clearing sparse stands first and follow up (strategy 4) is the best strategy. High budgets (> R2.8 million per year) are capable of clearing alien plants from the Peninsula in less than 15 years under all conditions. All threat indices showed the same trends, although the endemic plant index was most sensitive to clearing strategy and annual clearing budget. Strategies that prioritise sites of high biodiversity value (strategies 5 and 6) mitigate the threat to native plant diversity best. This is because prioritising sites of high biodiversity does not increase the time taken to clear the Peninsula, but reduces the threat by clearing sites of high biodiversity value first. Although annual clearing budget has the strongest influence on the threat to plant diversity, prioritising clearing at high diversity sites (strategies 5 and 6) reduces the threat for a given clearing budget. The shapes of the curves show that even a moderate annual

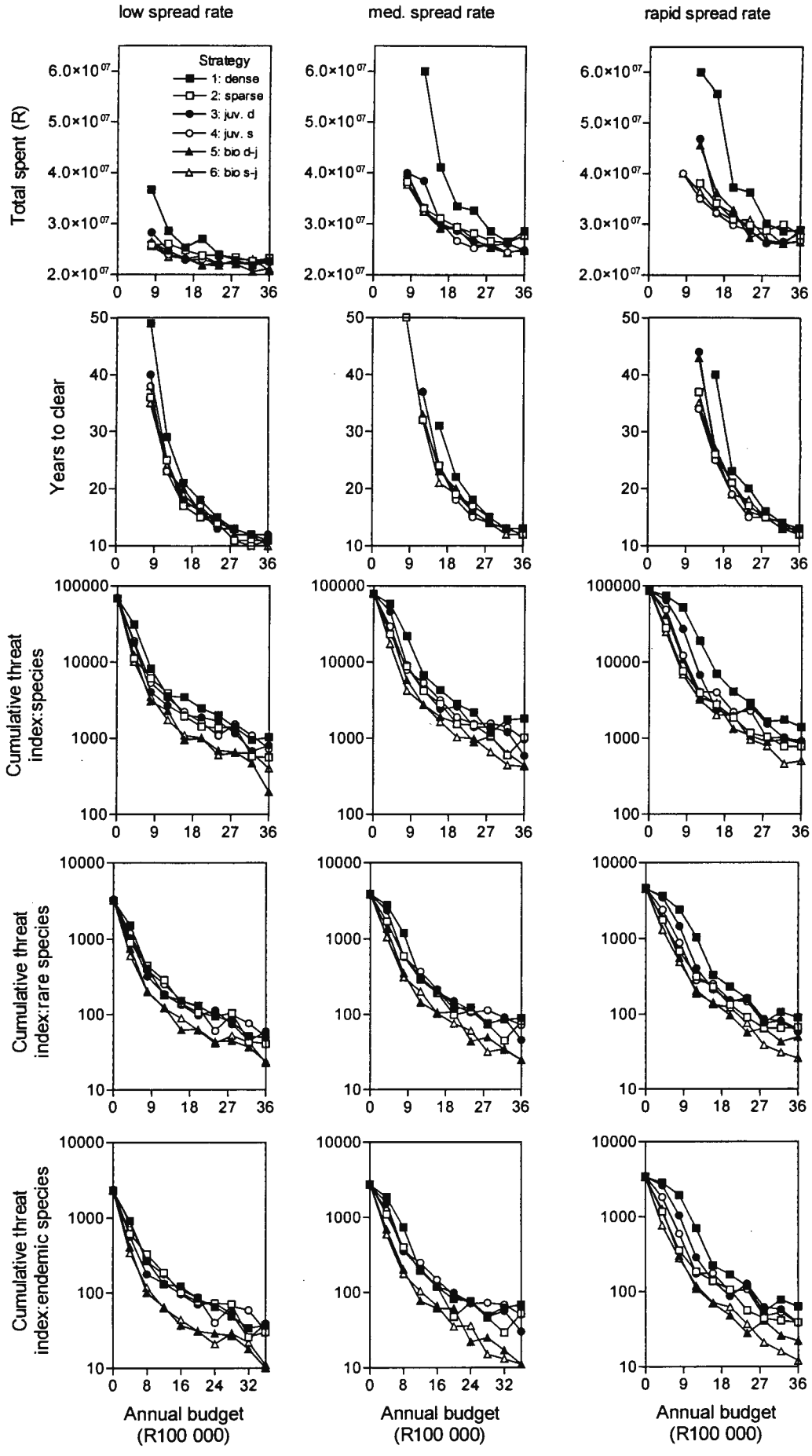

Figure 4. The effect of different clearing strategies and annual clearing budgets on the total amount spent on a clearing operation, the years it takes to clear, and the cumulative threat to native, rare and threatened, and endemic plant species on the Cape Peninsula. Each scenario was run for a low spread rate, medium spread rate and rapid spread rate as defined by the parameters in Table 1. The clearing strategies differ in how they prioritise clearing. Strategy 1 prioritises dense alien stands; 2 sparse stands; 3 juvenile stands and then dense stands; 4 juvenile stands and then sparse stands; 5 a weighting of high plant diversity value, immature, and dense stands; 6 a weighting of high plant diversity, immature and sparse stands (see Methods – alien plant clearing).

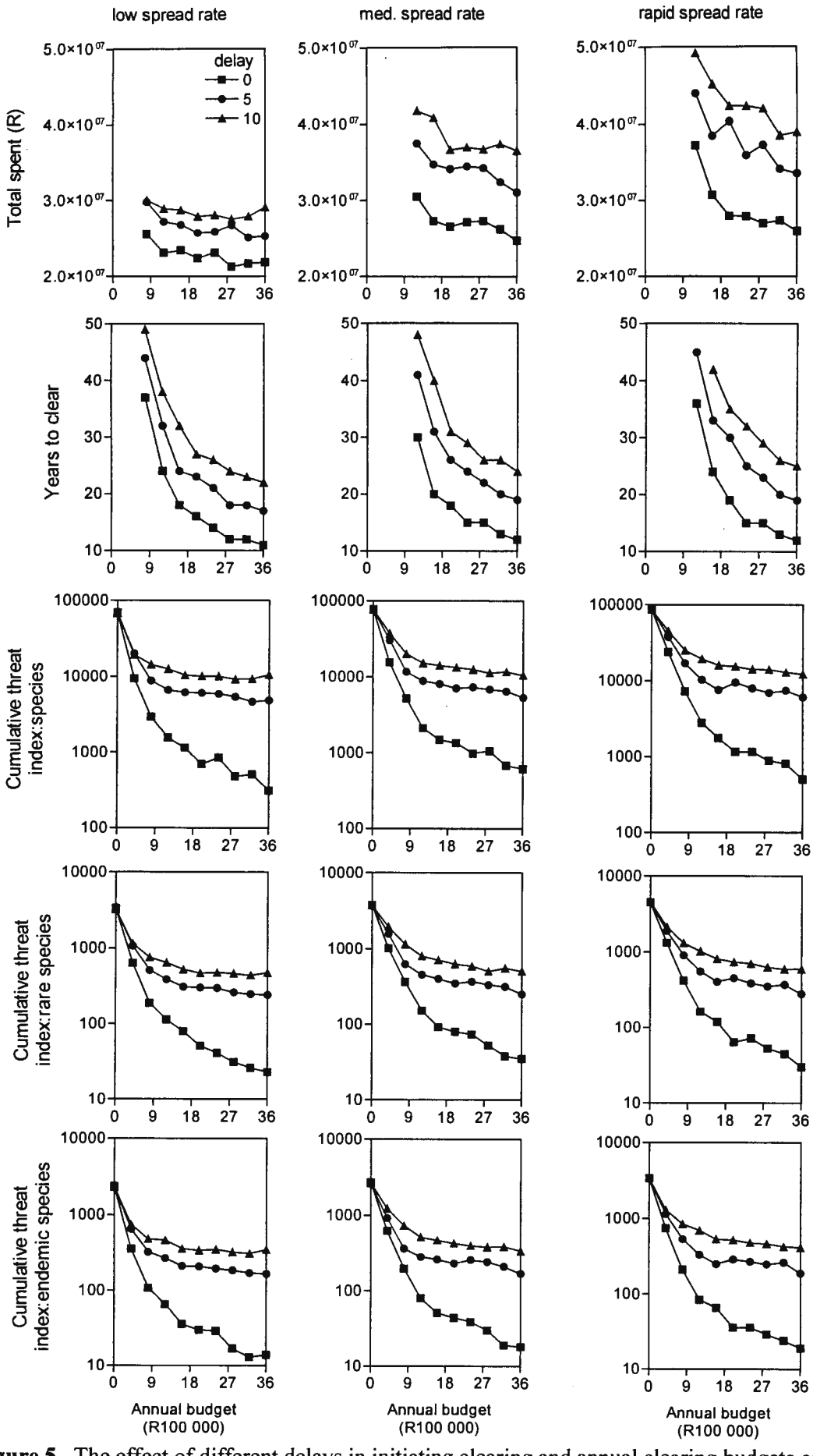

Figure 5. The effect of different delays in initiating clearing and annual clearing budgets on the total amount spent on a clearing operation, the years it takes to clear, and the cumulative threat to native, rare and threatened, and endemic plant species on the Cape Peninsula. The strategy that prioritised low-density sites of high biodiversity value and did follow-up clearing (strategy 6 see Methods – alien plant clearing) was used for all these scenario runs. Each scenario was run for a low spread rate, medium spread rate and rapid spread rate as defined by the parameters in Table 1.

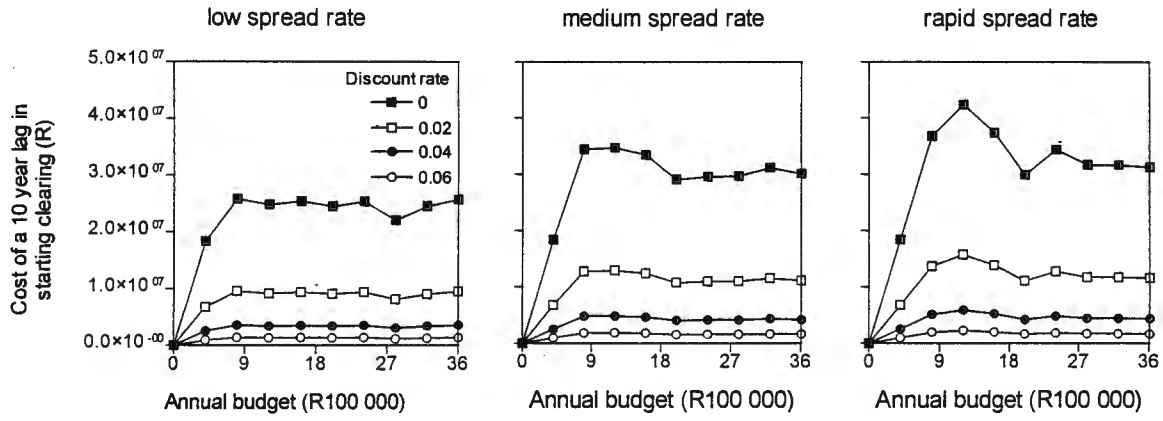

Figure 6. The present cost of a 10 year delay in starting clearing for different annual clearing budgets. The strategy that prioritised low-density sites of high biodiversity value and did follow-up clearing (strategy 6) was used for all these scenario runs. Each scenario was run for a low spread rate, medium spread rate and rapid spread rate as defined by the parameters in Table 1.

clearing budget can substantially mitigate the threat. This suggests that even if funds are limited, strategic effort can reduce the threat to plant diversity. Strategies that ignore biodiversity do not differ substantially in their ability to mitigate the threat to native plants. Moreover, the strategies that do prioritise high diversity sites (strategies 5 and 6) do not cost more; these strategies also do not increase the time taken to clear. For this case study it seems that the most cost-effective, rapid and biodiversity friendly strategy is strategy 6, which clears young and sparse stands with high biodiversity value first.

The cost of delaying the initiation of clearing operations is illustrated in Figure 5. The total amount spent increases with the delay period for all scenarios that manage to clear aliens within 50 years. Larger annual budgets slightly reduce the cost of delaying. The cost of a 10-year delay is R25 million for the low spread rate; R34 million for the medium spread rate and R40 million for the fast spread rate (Figure 6). The incentive for policy makers to delay the release of funding lies in the discounted cost of this delay. Figure 5 shows how the discount rate adopted influences the present value of not delaying. Lower discount rates are usually recommended for environmental projects (Pearce and Turner 1990, Perman et al. 1996). The results suggest that policy makers that use discount rates greater than 0.04 will have a limited perception of the cost of delaying clearing operations. Delaying the initiation of clearing also increases the annual budget needed to meet a clearing target. For instance a five year delay increases the annual budget needed to clear within 20 years from R1.6 to R2.8 million per year for the slow spread scenario, and from R1.6 to R3.6 million for the medium and rapid spread scenarios. A ten year delay increases the annual budget needed to

clear within 30 years from R1.0 to R1.8 million for slow spread, from R1.2 to R2.2 million for medium spread, and from R1.4 to R2.2 million for rapid spread. A lag in initiating clearing increases the threat to native plants; all three threat indices show this trend. Higher annual budgets cannot mitigate the cost of delaying the start of clearing.

DISCUSSION

Scaling up from local scale knowledge and data on ecological processes to landscape scale predictions is a central theme in landscape ecology. The variety and complexity of ecological processes means that there is no single protocol for scaling up. In this chapter I illustrated how an individual-based spatial simulation model can be scaled up to a landscape-extent simulation model. This scaling up process involved aggregating the behaviour of a fine-scaled model (Chapters 3,4,5,6) to a coarser grid resolution and integrating sub-models that simulate landscape-extent processes. Two landscape-extent sub-models were integrated: the first was a statistical description of site preference, the second was a simple fire spread model. The aggregation component of the scaling up protocol involved aggregating the behaviour of individual plants into even aged stands. The event-driven nature of recruitment and mortality and the consequent even-aged stands characteristic of the fynbos shrubland modelled here makes this an acceptable approach. In cases where the dynamics of the system being scaled up are continuous, this approach is not likely to be successful. In such cases, alternative scaling procedures will be needed (e.g. Acevedo et al. 1995, Pierce and Running 1995, Li and Reynolds 1997). In fact, because different processes will prose different constraints to the scaling processes, most scaling up protocols will be case specific; this study illustrates a simple protocol that is appropriate for event-driven systems characterised by even-aged stands of plants.

The scaling up process allowed us to make predictions at the landscape-extent. The landscape-extent management model was used to investigate the potential impacts of alien plants on native ecosystems. I used the invasion of the species-rich Cape Peninsula, South Africa as a case study. The results suggested that if left unchecked, alien plants could spread at a rate of between 0.03 and 0.085 % per year and cover between 75 and 95 % of available habitat on the Cape Peninsula in 50 years. The spread rates are similar to those reported for these from historical reconstructions made at a local scale in a range of fynbos ecosystems (Chapter 6). The exploration of different strategies for clearing plants showed that strategies that cleared dense stands first were expensive and took longer to eradicate

alien plants. The most rapid and cost-effective strategy was to start by clearing low-density stands of juvenile plants, then clear higher density stands of juvenile plants and leave high density stands of adult plants until last. This result agrees in spirit with the conclusion of a theoretical model that small outlying stands should be cleared first (Moody and Mack 1988). The advantage of this model is that it can be used to evaluate the monetary value of this increased efficiency for a real landscape and quantify how ecological processes influence the effectiveness of different strategies. The results also showed that the greater the clearing rate the less the total cost of the clearing operation. In addition for a population spreading at a given rate, a critical clearing rate exists: clearing above this rate does not significantly reduce the total cost of the clearing operation.

In fynbos the presence of alien plants severely threatens the survival of native plants (Richardson et al. 1989, Musil 1993); it follows that the rationale for clearing operations is to reduce this threat (Higgins et al. 1997). However, most clearing operations are evaluated on a purely financial basis. In this study I quantified threat using a cumulative threat index, which counts the number of years that alien plants cover a critical proportion of a native species' range. This allowed the definition of the clearing strategy that mitigates the threat best. While strategies that cleared sites quickly mitigated the threat, strategies that prioritised sites of high biodiversity value were even better. Importantly, the total costs of the biodiversity prioritisation strategies were not significantly higher than the cheapest strategies.

The scenario analyses showed that delaying the initiation of clearing had the strongest effect on the total cost of clearing and on the ecological impacts to native plants. The motivation for policy makers to delay the release of funding for clearing lies in the discount rate. I showed that for the discount rates that are commonly recommended for evaluating conservation projects (ca. 0.03; Pearce and Turner 1990, Perman et al. 1996), that the incentive for delaying is weak. However, the threat to native plants is cumulative; this means that the impact on plant diversity caused by delaying clearing cannot be mitigated through higher annual clearing budgets. The high cost and uncertain success of projects that aim to restore locally extinct populations in fynbos (Holmes and Richardson, in press) and the large number of species involved suggests that delaying clearing cannot be justified.

I know of no other studies that have used the reserve design concepts of vulnerability and irreplaceability (Pressey et al. 1996) to dynamically manage threats to biodiversity. Other

workers have concentrated on describing how management plans may influence the dynamics of target organisms (e.g. Liu et al. 1995). Future work should be dedicated towards linking models that predict the spatial dynamics of threat with the biological response of target organisms. Such models are likely to be of considerable value in planning the adaptive management of wide range of natural resources. Global change is going to radically reshuffle the potential and realised distributions of biota in the next 100 years; this suggests that a capacity to strategically plan management interventions in dynamically changing landscapes is going to be essential for maintaining biodiversity.

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CONCLUSION: PREDICTING RATES AND PATTERNS OF ALIEN PLANT SPREAD

INTRODUCTION

The aim of this thesis was to develop a protocol for predicting rates and patterns of alien plant spread. This was done using the invasion of fynbos ecosystems by pine trees and acacia shrubs. In this chapter I aim to briefly:

1. Summarise the steps involved in developing a protocol for predicting rates and patterns of alien plant spread.
2. Comment on the potential of applying this protocol to other systems.
3. Discuss how applied research problems can drive the interplay between data, theory and prediction.

A PROTOCOL FOR PREDICTING RATES AND PATTERNS OF ALIEN PLANT SPREAD

The protocol developed for predicting rates and patterns of alien plant spread is summarised in Figure 1. To predict the rate and spread of an alien plant population one needs to understand the ecological processes involved in the invasion (Chapter 2). Essentially this involves defining the environmental conditions under which a species can grow, reproduce and disperse. This means that context-specific information is needed to predict which species will invade which environments (Chapter 4). To make quantitative predictions of rates and patterns of alien plant spread, this knowledge needs to be translated into a set of operational functions (Chapters 3 and 4). I found that spatially explicit individual-based simulation models provided a flexible framework for integrating a range of functions into a single model. Before field data are collected, the sensitivity of the model should be explored. This should explore how the structure of the model and hence the implicit assumptions of the model influence the model's predictions. Chapter 3 does this by comparing the behaviour of the simulation model to the classic reaction-diffusion model of spread and explores how the spatial grain of the model influences its predictions. The model should also be parameterised using a range of parameter levels that are defined by existing data, knowledge and uncertainty (Chapter 3). This process should inform the modeller whether the structure of the

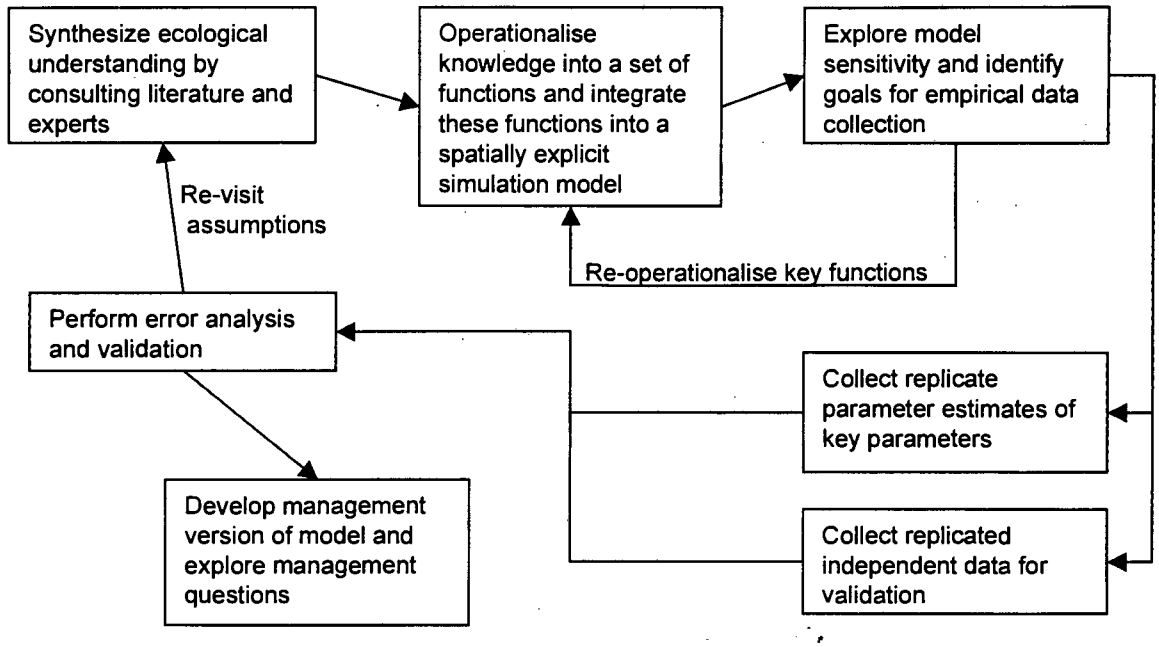

Figure 1. Outline of the protocol for predicting rates and patterns of alien plant spread developed in this thesis

model is appropriate. Importantly the sensitivity analysis will provide clear goals for empirical data collection. The sensitivity analysis can also identify any major flaws in the way key processes are modelled. In this study I identified that existing methods for simulating dispersal were flawed. This meant that the dispersal functions had to be redesigned (Chapter 5). The next step in the protocol is to collect the important data identified by the sensitivity analysis (Chapter 6). Ideally independent data to validate the model should also be collected at this stage (Chapter 6), although appropriate data are unavailable in many situations. The range of predictions made by the model for the different empirically based parameterisations should be explored, and these predictions should be compared with the independent validation data (Chapter 6). After the validation procedures, the fundamental assumptions of the model should be revisited. A successful validation may provide correlative support for the models assumptions; an unsuccessful validation would suggest that the assumptions of the model should be re-evaluated. If all has gone well there should be enough confidence in the model's behaviour to use the model to explore a range of management questions. In this study, developing a management version of the model involved scaling up the model to the landscape extent (Chapter 8); depending on the management questions involved, this scaling up process may not be necessary.